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LOCOMOTOR MORPHOLOGY
OF THE VAMPIRE BAT,
DESMODUS ROTUNDUS

ALTENBACH

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LOCOMOTOR MORPHOLOGY
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LOCOMOTOR MORPHOLOGY
OF THE VAMPIRE BAT,
DESMODUS ROTUNDUS

By

J. SCOTT ALTENBACH

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ALBUQUERQUE, NEW MEXICO 87131

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FOREWORD

ONE obvious objective of any functional morphological study is to determine how anatomical features operate. Far more important, however, is the interpretation of the adaptive significance of those anatomical features and the role their functioning plays in the evolutionary, as well as the day-to-day, biology of an organism. Although morphological features have been used widely for taxonomic purposes for centuries, only relatively recently has interpretation of the functional significance of morphological features been applied toward understanding the biology of organisms. That this is especially true of locomotor morphology is somewhat surprising, because locomotion plays such a critical role in the survival of the vast majority of heterotrophic organisms.

Few, if any, groups of animals have as broad a spectrum of locomotor styles as do mammals. Certainly much of their abundance and general success has been a function of evolution of such diversity in locomotor mechanisms. The locomotion of bats is especially interesting, because both pelvic and pectoral limbs are used in aerial as well as terrestrial locomotion. Evolutionary compromise has variously placed different bats on a spectrum between extreme limb modification for certain types of flight and modification for more efficient terrestrial locomotion.

The study of a biological extreme, whether it is a community, an organism, or a functional system within an organism, can often clarify the mechanisms of operation of the average or less extreme. This is particularly true in the study of bat locomotion where the outstanding locomotor specialization, flight, is rather poorly understood. The common vampire bat (*Desmodus rotundus*) is an ideal candidate for locomotor morphology studies because it represents an extreme in locomotor specialization. It seems logical that a flying machine can vary or be modified evolutionarily in relatively few ways and still fly. The vampire bat has seemingly approached the limit of evolutionary modification by specializing in rapid and effective terrestrial locomotion while retaining the ability to fly. A functional morphological investigation of the vampire bat as a flying machine should not only clarify the flight mechanics of other, less extreme, bats, but also facilitate interpretation of the role of flight-associated morphology. Of equal interest is the study of the terrestrial locomotor modifications that make the vampire so extreme.

My study of the locomotor morphology of the vampire was undertaken both to interpret the functional significance of its locomotor-associated anatomy to provide another viewpoint in our biological knowledge of this animal and to stimulate others to add additional interpretation of functional morphology to bat biology, as well as to the biology of other organisms. Only description of the anatomical details of the pectoral girdle and limb is included in this work. Admittedly the pelvic girdle and limb are important in locomotion in the vampire bat and show specializations for its unique locomotor mechanisms. However, I feel that the most spectacular of the anatomical specializations for terrestrial locomotion and certainly the most important specializations for flight are those of the pectoral limb and girdle, and I have thus focused my attention on these structures. Perhaps this work will stimulate publications of functional morphological data on the pelvic girdle and limb.

I want to thank Terry Vaughan for his encouragement at the onset of this study. Paul Baldwin, Rowan Frandson, Thomas Bahr, and Y. Z. Abdelbaki gave encouragement, generously loaned equipment, and read the manuscript as prepared as a doctoral dissertation. Marilyn Altenbach contributed countless hours in help with surgical procedures, typing, and proofreading the manuscript. Without her assistance and encouragement this work would not have been possible. Sincere thanks are due to the personnel of the U.S. Fish and Wildlife Service at the Denver Wildlife Research Center for the generous loan of living vampire bats and to Northern Arizona University for the loan of preserved specimens. I deeply appreciate the help of Janice Moore and Lyle Berger, who read proof of the final manuscript, and want to thank James Findley, Patricia Freeman, and Michael Bogan, who critically read portions of the manuscript. I also thank James N. Layne for his encouragement and his very time-consuming editorial work, and Lorene Deckert who typed the final manuscript.

I would like to dedicate this monograph to my major professor, the late Robert R. Lechleitner. He was the finest teacher I have ever known and I can only hope to be a scientist of his competence and a human being of his kindness. To his family I express sincere thanks for the kindness and generosity shown to me and their encouragement of my research.

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INTRODUCTION

ALTHOUGH bats have been studied intensively for many years, relatively little has been learned about the mechanisms of locomotion and the anatomical features involved with locomotion in this large order of mammals. The preliminary work in the field of chiropteran locomotor morphology is restricted to relatively few species of bats and emphasizes the need for investigation of anatomical specialization and, particularly, the modes of locomotion in other species.

Cuvier (1800, *et seq.*), Kolenati (1857), and Humphry (1869) published papers on bat anatomy, but Macalister (1872) was the first to standardize anatomical terminology for this order and to correct errors of earlier investigators. Macalister described the myology of 19 species representing the families Pteropidae, Rhinolophidae, Megadermidae, Phyllostomatidae, and Vespertilionidae, and his work remained the major reference in chiropteran myology until 1959. Maisonneuve (1898) described the osteology and myology of *Vespertilio murinus* and Levy (1912) described the myology of the upper arm and shoulder of 16 species of bats. Petersen (1923) studied the osteology of the arm and carpus of *Vespertilio murinus*. Eisentraut (1936) published photographs of *Myotis myotis*, *Rhinolophus hipposideros*, and *Plecotus auritus* in flight, and presented the first analysis of the mechanics of flight in bats. He carefully described the phases of the wingbeat and determined where thrust and lift were generated. Although the photographic material available to him was of poor quality, he was able to recognize that interspecific differences exist in flight mechanisms and that different types of flight observed in a single species require different movements.

Vaughan (1959) correlated differences in limb and girdle morphology with differing modes of flight, terrestrial locomotion, and roosting habits. This publication standardized chiropteran myological terminology and has remained the major reference on chiropteran locomotor morphology. Later publications by Vaughan (1966, 1970a, 1970b, 1970c, 1970d, 1970e) further illustrate anatomical specialization to fit a particular mode of locomotion or behavior. Struhsaker (1961) attempted to correlate interspecific differences in flight patterns with differences in relative weights

of specific flight muscles and the dimensional relationships of the flight membranes. However, incorrect analysis of the mode of flight of one species makes certain of his conclusions questionable. His paper does provide dimensional relationships that are valuable for comparison. Hartman (1963) calculated dimensional and dimension/weight ratios for 12 species of bats, including the vampire bat, of five families. His data are useful for comparison and show interesting aerodynamic relationships. Gaisler (1964) published observations on the flight of several European species and confirmed some of the conclusions of Eisentraut. Findley *et al.* (1972) presented data on morphologic properties of bat wings and speculated on their functional significance.

Altenbach (1968) described the appendicular anatomy and flight of a hovering species (*Leptonycteris sanborni*) and compared them to those of a species (*Eptesicus fuscus*) that flies rapidly and cannot hover. The contrasts clarified the significance of many anatomical features of both species. Walton (1968) described the appendicular osteology in members of the family Phyllostomatidae. This paper did not consider functional significance but is a valuable anatomical reference for this family. Vaughan and Bateman (1970) correlated differences in foraging behavior with variations in forelimb morphology in the families Mormoopidae and Phyllostomatidae.

Norberg (1970a, 1970b) published a beautifully illustrated description of the osteology and myology of the pectoral limb of *Plecotus auritus*, and an account of hovering flight in this species. Norberg (1969) also discussed the bracing system that is seen in the leading edge of the "hand-wing" of bats.

The difficulties encountered photographing small flying animals in anything but highly restrictive enclosures are severe. Virtually no detailed research on bat locomotion has been attempted except by Eisentraut (1936), and the data he had to work with did not allow thorough analysis of the mechanisms involved.

Much of the literature concerning bat locomotion, particularly flight, is based on indirect evidence. Dimensional relationships of flight membranes, dimension/weight relationships, positional relationships of myological and osteological components of the girdles and appendages, and visual observations of bats in flight and terrestrial locomotion can lead to reasonably accurate conclusions about the mechanics of locomotion. However, only high-speed photography can clearly illustrate the mechanisms involved and

the often subtle interspecific differences. When high-speed photographic data are available, anatomical features can be correlated with movements that are peculiar to specific types of locomotion.

The objectives of this study were: (1) to analyze through the use of high-speed still and motion picture photography the mechanisms of walking, hopping, jumping, climbing, and flight used by *Desmodus rotundus*; (2) to describe the pectoral girdle and the appendicular osteology and myology by dissection of preserved specimens and examination of skeletons; (3) to determine how some of the muscles involved with locomotion function during normal movements by simultaneous photography and electromyography; (4) to determine the functional significance of pectoral girdle and appendicular anatomy in the locomotion of *Desmodus*; and (5) to determine, if possible, the significance of specialized locomotor behavior in *Desmodus*.

It is surprising that the locomotion of the common vampire bat has not heretofore been investigated in detail and that not more than a cursory examination of its appendicular anatomy has been attempted. In contrast, the distribution, feeding behavior, and particularly the role of this species as a vector of disease of man and domestic animals have been the subject of many published accounts.

The agility and delicate walking behavior of this species were described by Beebe (1927) and Price (1950) from observations made on vampires attempting to feed on them. Ditmars and Greenhall (1935, 1960) related the account of an explorer who noted that *Desmodus* "walked" or "hopped from one spot to another." These authors described the ability of vampires to walk, climb, and jump into flight from the ground and published the first photographs of the terrestrial locomotion of this species (Ditmars, 1934; Ditmars and Greenhall, 1935, 1960). The photographs illustrate the characteristic walking gait of the bat, the posture when drinking from a dish, and the feeding posture on the back of a live goat. The authors commented that *Desmodus* moved rapidly over the back of the goat to avoid being brushed off as the animal walked under obstacles.

Dalquest (1955) noted the extreme terrestrial agility of *Desmodus*, its ability to hop and to jump into flight from the ground, and its characteristic swift and direct flight. Wimsatt (1959) noted that *Desmodus* could rapidly "scramble" across vertical surfaces and used

hopping and leaping jumps in terrestrial locomotion. He also remarked on its strong, swift flight and its habit of flying within a meter of the ground. Mohr (1955) also mentioned the agility of this bat and the "crab" or "spider-like" way it moves over vertical surfaces. He also observed vampires taking flight from the ground after being knocked from a roost by the blast of a gun. Leen and Novick (1970) referred to the jumping behavior of *Desmodus* and published photographs of individuals standing and jumping.

Many authors have suggested that the terrestrial locomotor ability of the vampire is useful in feeding behavior but provide only scant evidence to support this hypothesis. An account by Hensel (1869) stated that in South America cattle are bitten by *Desmodus* about the hooves, and recent evidence from México (Mitchell, 1970; Robert Tigner, personal communication) indicates that individuals often feed from the ground by biting cattle on the fetlock and, if necessary, follow the animal while taking blood from the wound. The agility and the ability to jump appear necessary to avoid being crushed while feeding and to take flight from the ground. Motion pictures taken by A. M. Greenhall show *Desmodus* feeding on unrestrained guinea pigs and illustrate the use of the terrestrial agility and walking behavior to catch and feed on these active rodents.

Although a few other species of bats move readily on the ground (Burt, 1934; Vaughan, 1959, 1970*d*; Leen and Novick, 1970) and some can take off from the ground (Eisentraut, 1936; Vaughan, 1959; Anonymous, 1969), no other species possesses the extreme terrestrial agility and jumping ability of *Desmodus*.

MATERIALS AND METHODS

Preservation and Dissection

TEN *Desmodus rotundus* from near San Blas, Nayarit, and eight from near Mazatlán, Sinaloa, were preserved in 10 per cent formalin and stored in 70 per cent ethyl alcohol. Additional frozen specimens were obtained from the Denver Wildlife Research Center of the U.S. Fish and Wildlife Service and were preserved and stored in the same manner.

Several preserved bats were dissected under a binocular microscope with variable magnification from seven to 30 power. These bats were stored in a solution of one part glycerin and eight parts 70 per cent ethyl alcohol, which prevented desiccation and softened muscles. Photographs of the dissections were taken with a 35 mm camera for aid in preparation of anatomical drawings.

Skeletons of a male and a female bat from the collection of Northern Arizona University were used for a description of osteological features. A bat from Nayarit, México, was cleared in two per cent KOH solution, stained with Alizarin Red S, and stored in glycerin for use in description of osteological features of the carpus. X-ray photographs of another of the Nayarit specimens were taken by Y. Z. Abdelbaki of the Anatomy Department, Colorado State University, for preparation of anatomical drawings.

Photographic Procedures

Patterns of terrestrial and aerial locomotion were analyzed by means of high-speed still and motion pictures. Bats used in this phase of the study were maintained in the laboratory on a diet of defibrinated beef blood and housed in separate containers made from 2-liter freezer cartons.

All still photographs were taken with a Praktiflex 35 mm single lens reflex camera on Kodak Panatomic X film with illumination provided by a 100 watt second electronic flash unit of my own design. The $\frac{1}{15000}$ second flash eliminated blur and permitted an aperture of f/16 with the three lamp heads positioned 50 cm from the bat. A black velveteen backdrop was positioned behind the flight path of the bat and the camera shutter was

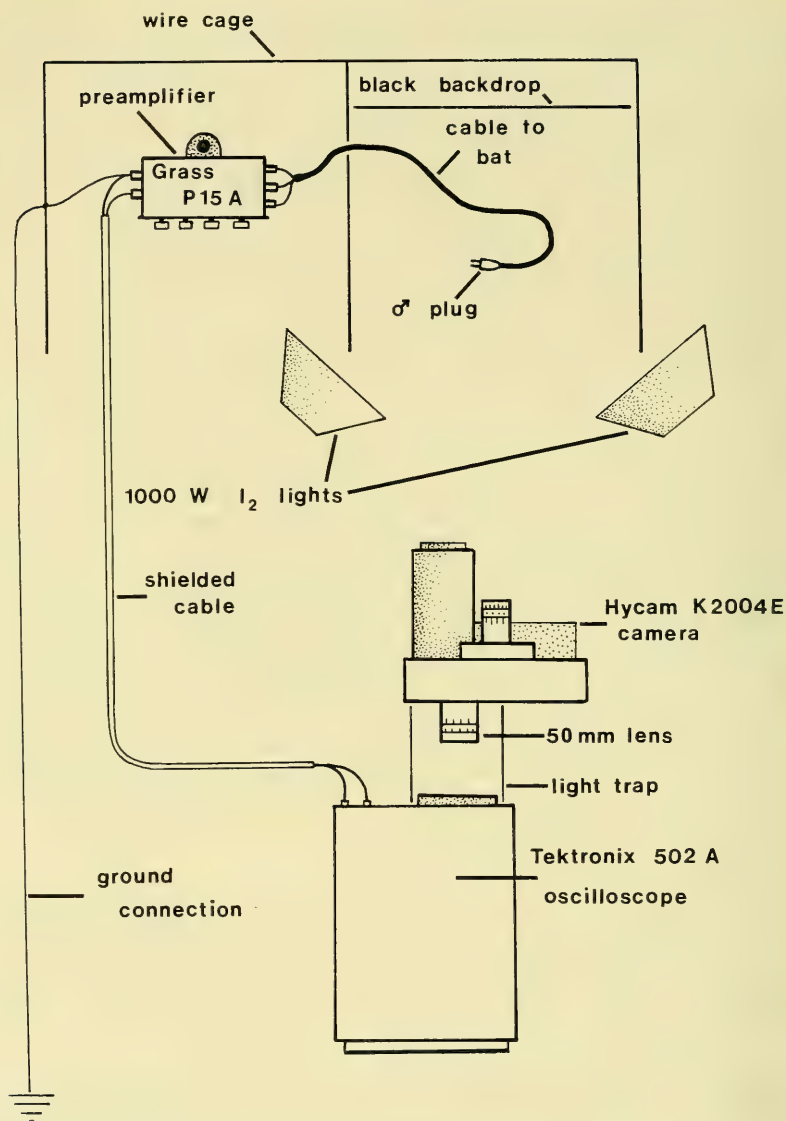


FIG. 1. Diagram of the equipment used in the electromyographic experiments. Two additional lights not illustrated were positioned above the wire cage. The plug and cable, preamplifier, and oscilloscope were not used in general high-speed photography of locomotion, but the position of the lights, wire cage, and camera was similar.

opened prior to the exposure. After the flash was triggered, the shutter was closed. Since light in the room was normally low, no fogging of the film occurred; the only exposure was produced by the $\frac{1}{15000}$ second flash. Photographs of the bats in motion were taken as they interrupted a light beam directed on a photocell that in turn activated an advance relay triggering the flash. Bats were directed into a prescribed area by baffles or released from beneath an inverted bowl. Photographs of bats standing and climbing were taken manually by use of a toggle switch that triggered the flash.

High-speed motion pictures were taken with a Hycam K2004E camera. Kodak Four-X reversal 16 mm film was used in 100-foot rolls and forced to ASA 800 during development. Four lights totaling 3400 watts output provided sufficient illumination to use an aperture of f/8 at 250 fps (frames per second), 5.6 at 500 fps, and 4 or 2 at 1000 fps. The bats were positioned under an inverted cup in an open-fronted wire flight compartment 0.6 m wide, 0.9 m high, and 0.9 m deep that was lined on the bottom and back with black velveteen. The camera was focused on the center of this compartment and the lights were positioned in front of it (Fig. 1). In photographing bats with this set-up, the lights were switched on, the camera started, then the cover pulled off the bat. Motion pictures of flight from the side were taken as the bat flew from baffles into a room.

Electromyography

To determine the temporal sequence of contraction of certain muscles during normal movements, stainless steel electrodes 0.001 inch in diameter were implanted in the muscles and exteriorized through an implanted silicone rubber plug (Altenbach, 1972). A two-conductor shielded cable 1 m long with a soft plastic insulator was adapted with a three-pin male plug for attachment to the female plug sutured to the bat. The contacts could be adjusted to allow separation of the plugs with a gentle tug, preventing injury to the bat when it moved beyond the length of the connecting cable. The cable connected to a Grass model P15-A AC preamplifier that provided a gain of 10, 100, or 1000 to the myopotential changes monitored in the bat. The connecting cable and preamplifier were arranged in a grounded cage of 6-mm hardware cloth

with the cable running through a wire partition (Fig. 1). A heavy shielded cable connected the preamplifier to a Tektronix 502-A dual beam oscilloscope.

The high-speed motion picture camera and lights were positioned in front of the cage as described in the section on photography. The objective lens was focused on the flight compartment of the cage and a 50-mm lens mounted on the rear focusing aperture was focused on the screen of the oscilloscope 60 cm behind the camera. This technique superimposed an electromyographic trace over the frame by frame record of the action in the cage. In this type of oscillography the cathode beam is not swept by a horizontal amplifier but is positioned in the center of the tube. The deflections are vertical and correspond, in this case, to potential changes in a muscle.

The camera was operated at 200, 250, and 500 fps for the electromyographic experiments, and the same film and processing described for motion picture photography were used. The oscillographic trace was transferred to paper tape for analysis by a device that moved the film and paper tape parallel to each other at different speeds. A stylus was moved to follow the vertical deflections in the myographic trace on the film, and a pen attached to the stylus transcribed the trace onto the paper tape. This method allowed the trace reproduced on the paper tape to be condensed horizontally to readable and reproducible proportions. For example, if the film was moved past the stylus at twice the speed of the tape, the trace on the film was condensed 50 per cent on the tape. Register marks were put on every fifth frame of the motion picture film and at corresponding points on the tape to correlate the myographic streak with the movements of the bat.

Because myopotential changes seldom exceeded 2 millivolts, a gain of 100 was sufficient for preamplification and the oscilloscope vertical amplifier was set at 50 millivolts/cm. Thus a potential change of 2 millivolts produced a 4-cm deflection of the electron beam.

Tracings were made from the films for illustration of the movements for correlation with the electromyographic traces. No timing marks were put on the film because the camera was speed regulated to ± 1 per cent and periodically checked for accuracy. Differences of 1 per cent are negligible and calculations of elapsed time can be made by frame counts. Slight differences in speed of

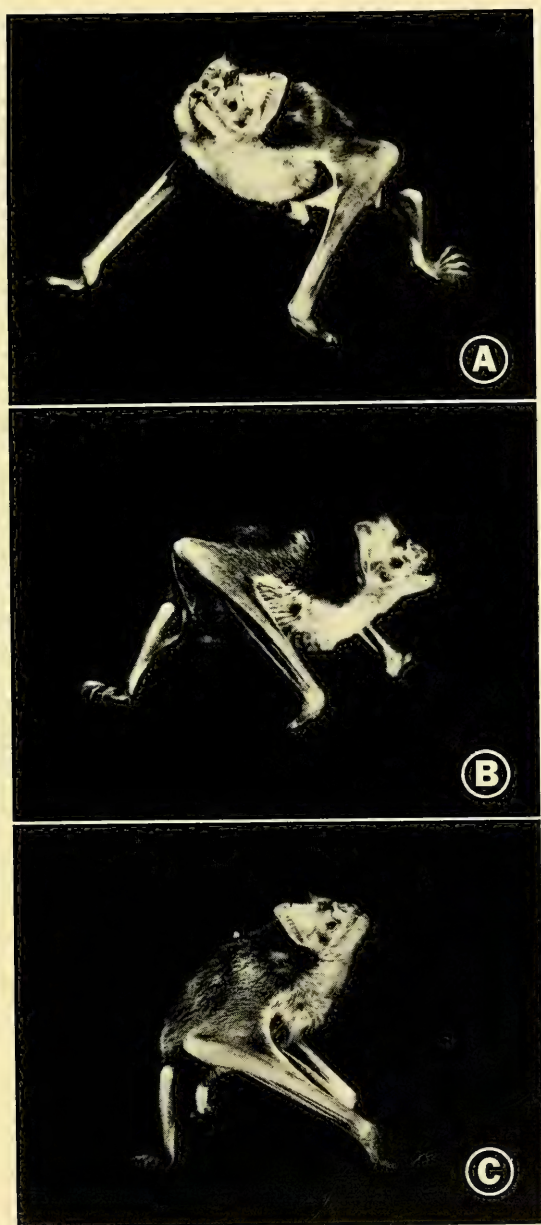


FIG. 2. Alert standing postures of *Desmodus rotundus*: A, inclined slightly; B, horizontal; C, steeply inclined.

the film do not affect the correlation of movement with myopotential changes inasmuch as the two are recorded simultaneously.

LOCOMOTION

Standing Postures

IN alert standing postures, *Desmodus* often holds the body 2 or 3 cm above the substrate and inclined upward between 10 and 50 degrees above the horizontal (Fig. 2A). The thighs are oriented laterally and the knees are flexed 60 to 90 degrees and usually oriented perpendicular to the substrate, with the feet directed posterolaterally. The weight of the hind body rests on the heel pads, the pads at the metatarsophalangeal junction, and perhaps on the claws, which are usually spread slightly. The brachii are directed posterolaterally and dorsally and the forearms are directed anterolaterally. If the body is not steeply inclined, the brachii are inclined up to 40 degrees above horizontal and inclined posterolaterally (Fig. 2B). The elbows are strongly flexed, and the forearms are oriented anterolaterally and inclined 50 to 60 degrees above horizontal. The thumbs are directed laterally, and the weight rests on the basal and distal thumb pads.

If the body is inclined more steeply, the brachii are adducted but still directed strongly posteriorly. The forearms are extended slightly and oriented strongly anteriorly and slightly laterally. Photographs of the bats in an inclined stance indicate that the first metacarpals are directed ventrally and the weight is concentrated on the distal thumb pads and phalanges, which are hyper-extended anteriorly and laterally from the metacarpal (Fig. 2C).

When feeding terrestrially on the fetlock of a large ungulate, the bat assumes a posture that is similar to that of the elevated stance in Fig. 2C (Mitchell, 1970). The hind limbs are almost fully extended as in a jump, occasionally so much so that the weight rests on the pads at the metatarsophalangeal junctions. The brachii are adducted and oriented ventrally in a plane parallel to a sagittal plane through the body. The elbows are fully extended, and the forearms are directed nearly vertically. The thumbs are often adducted in line with the long axis of the forearm, with the weight

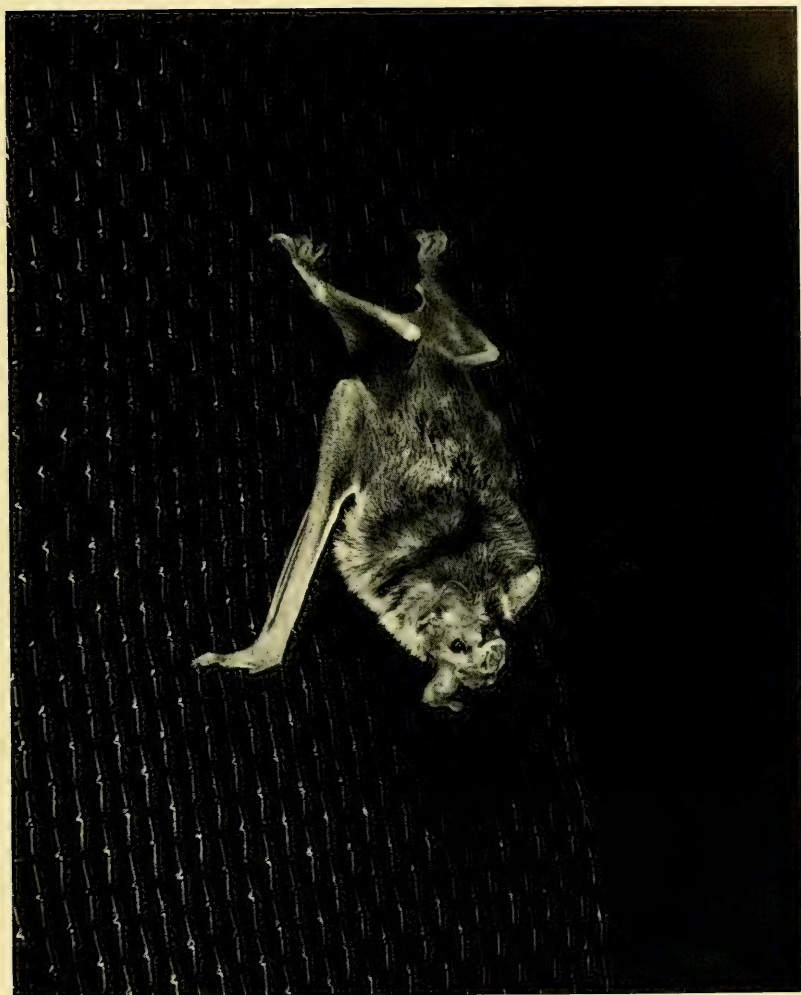


FIG. 3. Hanging posture of *Desmodus*.

resting on the terminal phalanges and claws as in Fig. 2C. The body is thus steeply inclined, and the lips can reach up to 8 or 10 cm above the substrate.

The transition from these postures, with the exception of the fully elevated feeding posture, to terrestrial locomotion is simple and involves only alternate strokes with the limbs.

Hanging Posture

When a bat is fully alert and hanging on a vertical surface, the body is held as far as a centimeter away from the surface and is inclined anteroventrally with the head sharply turned upward or directed toward an observer (Fig. 3). The thighs are oriented laterally and slightly dorsally, relative to the animal, and the shanks are flexed and directed upward, often slightly medially, and toward the vertical surface. The feet are oriented upward and the weight is on the claws which are slightly spread. The brachii are oriented posterolaterally at the level of midbody and the forearms are directed ventrolaterally. The thumbs are directed laterally or slightly dorsolaterally, with the weight supported by the basal pads and the claws. The inclination of the body and its position away from the surface tend to force the thumb toward the surface, using the hind feet as a fulcrum. This provides good traction for the forelimbs and allows sudden lateral or dorsal movements powered by the forelimbs.

A resting position is similar, except that the body is close to the surface and the forelimbs are not directed laterally. When the bat is resting pendant from a steeply inclined overhead surface with sufficient irregularities to give the claws purchase, the hind limbs often are fully extended and the forelimbs are flexed toward the brachium and not in contact with the surface. However, when the animal is disturbed in this position, the hind limbs are flexed, drawing the body toward the surface, as the forelimbs are extended posteriorly or ventrally, relative to the bat, to bring the thumbs in contact with the surface. This allows the forelimbs to be used in an evasive drop into flight or terrestrial locomotion.

Walking

The walking gait of *Desmodus* on a horizontal surface, like all other locomotion in this species, is highly variable, the particular pattern depending upon a number of factors. When unhurried, bats accustomed to captivity and observation walk in a deliberate and even gait. However, under experimental conditions, this type of walking was infrequently observed; the animals usually employed a faster walking gait. Analysis of films of slightly hurried locomotion of a bat approaching and starting up an inclined sur-

face indicates that at the start of a stride the hind limbs are flexed at the knee and oriented in reptilian fashion, with the plane of the limbs and feet directed posterolaterally (Fig. 4A). The brachii are inclined posterodorsally and the forearms are partially flexed, with the carpi and thumbs contacting the substrate roughly two cm lateral to the sides at midthorax. The body is about a centimeter above the substrate at the start of the stride. The hind limbs are extended at the knees as slight adduction of the brachii and extension of the right elbow lift the body and shift it to the left (Fig. 4B–C). Extension of the left hind limb continues as the right hind limb is lifted by abduction of the femur and slight flexion of the knee and brought anteriorly (Fig. 4C–D). Almost concurrently the left forelimb is lifted off the surface and extended forward and to the left (Fig. 4D). Within eight milliseconds the right forelimb is lifted after a lateral and posterior thrust and is brought forward by flexion of the elbow (Fig. 4D–F). Only the right hind limb remains in contact with the substrate, and extension of the right knee and a posterior swing of the femur provide forward thrust to the body. The right hind limb reaches the end of its forward swing and contacts the substrate as the left forelimb contacts the inclined surface toward which the bat is walking (Fig. 4F). Simultaneously the left hind limb is raised by abduction of the femur and begins a forward swing. Meanwhile, the left forelimb begins to pull the body forward and up the incline by movement of the brachium, which draws the distal end of the partially flexed forearm downward and posteriad (Fig. 4F–G). The right forelimb contacts the substrate, and extension of the forearm and slight adduction of the brachium drive the body forward and toward the incline (Fig. 4H–I). The right hind foot is raised and swung forward as the bat pushes off the substrate with an extension of the left hind limb followed by a powerful adduction or flexion of the right thumb (Fig. 4I–K). As the right thumb is adducted, the left forelimb is lifted and the bat becomes airborne for about 10 milliseconds (Fig. 4L–M). The right hind foot is extended laterally and ventrally to contact the substrate simultaneously with the left forelimb. The left hind limb reaches the end of its anterior swing and, with the knee flexed, contacts the inclined surface as the right forelimb contacts the substrate after flexion of the elbow to advance the arm. Both hind limbs extend, along with extension of the elbow and inclination of the brachium of the right forelimb, to thrust the

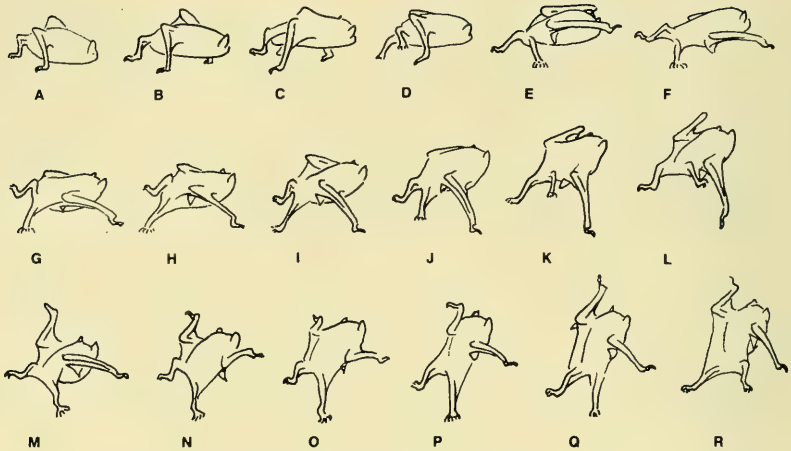


FIG. 4. Drawings at 40 millisecond intervals of *Desmodus* walking rapidly on a horizontal surface (A-H) and up an incline (I-R).

body up the incline, while the left forelimb is extended forward to grasp higher up (Fig. 4N-R).

After the series of pictures upon which this description is based was taken, the bat executed a turn on the inclined surface and used the typical backward climbing method to climb it vertically.

Hopping Locomotion

When *Desmodus* further accelerates its movement on a horizontal surface, a hopping gait is employed, which leads to a rapid leaping type of locomotion if a sufficiently open expanse of substrate is available. Fig. 5A-E illustrates a turn prior to the initiation of hopping locomotion. The bat pivots to the right around the right hind foot by the force of the left forelimb pushing against the inclined surface immediately behind (Fig. 5A-C). The left hind limb is raised, pulled forward, and positioned lateral to the body (Fig. 5C-D). As the right forelimb is moved laterally during the last of the turn, the right hind limb is lifted slightly, and when the forelimb contacts the substrate, the right hind limb is powerfully extended (Fig. 5D-G). Both brachii are inclined and the forearms are extended to drive the body forward and upward. The left hind limb

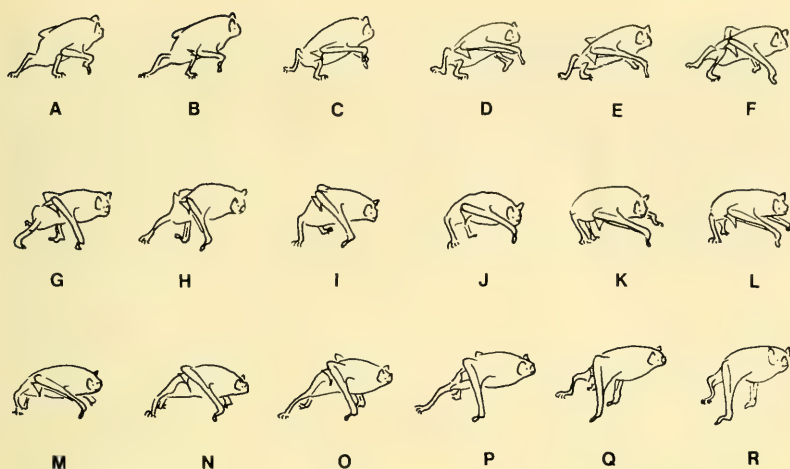


FIG. 5. Drawings at 40 millisecond intervals of *Desmodus* in typical hopping locomotion on a horizontal surface.

is raised as the right hind limb is extended, and both are pulled strongly forward. The forelimbs leave the substrate after the terminal adduction of the thumb for thrust and the bat is airborne for about 70 milliseconds (Fig. 5H-K). The forelimbs are then moved upward by adduction of the brachium and then anteriorly by simultaneous adduction, supination, and subsequent anterior swing of the brachii. The bat alights simultaneously on the antero-laterally directed hind feet and ventrally oriented thumbs (Fig. 5L).

Transition to a more vigorous hopping locomotion is accomplished when the bat maintains forward momentum by inclination of the brachii and extension of the elbows (Fig. 5M-Q). The thighs, which were partially abducted as the bat alighted, are swung posteriorly, and the knee is extended to drive the body forward and upward, much as in a jump into flight. The hind feet leave the substrate as the forearms are extended (Fig. 5P-Q). A slight adduction of the brachii, with the forearms extended at right angles to them, provides upward momentum to carry the bat higher than in the previous hop. The thumbs are not forcefully flexed as the forelimbs leave the substrate, as in a typical jump. In addition, the weight is transferred from the thumb pads to the anterior surface of the carpi when the forelimbs are inclined.

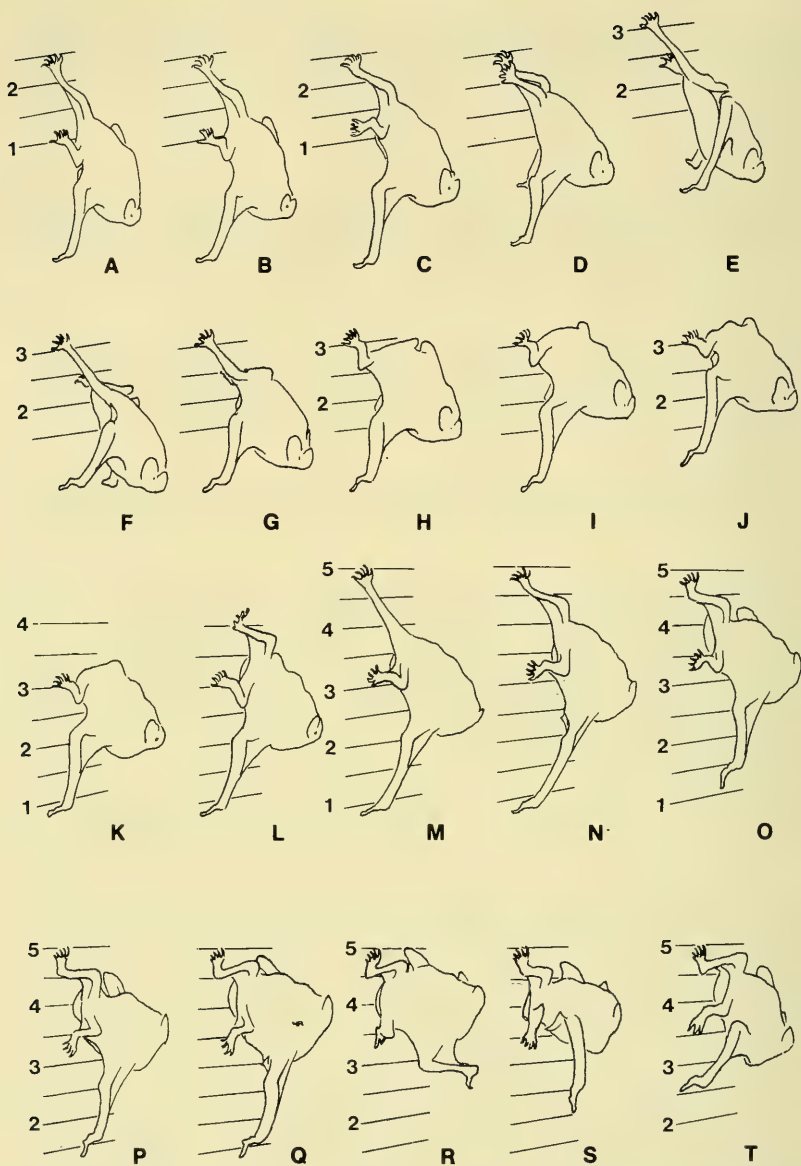


FIG. 6. Drawings at 44 millisecond intervals of *Desmodus* climbing on a vertical surface. Horizontal lines (1-5) on the surface behind bat are included as spacial reference points.

Hopping locomotion can carry the bat over a horizontal surface at rates of up to two m per second with surprising agility. The animal can readily hop over or around obstacles in its path with little noticeable reduction of speed. The hopping locomotion often alternates with short flights varying from slightly less than half a meter to several meters in length and 0.3 m or less in height. Often, only two or three hops are made between these flights. If there is an unobstructed path ahead of the bat, continuous forward flight is initiated by a more powerful jump.

Climbing

Although able to climb a vertical surface forward or sideways, *Desmodus* normally climbs backward, and, if hurried, slightly sideways. I have observed this behavior in the wild as well as in the laboratory. The bats are exceptionally alert while climbing. The presence of an observer may influence the frequency of backward climbing, as this form of locomotion allows the bat a good view of the observer. Thus it is possible that when undisturbed, vampires may use other types of climbing. However, this seems unlikely. The following description of backward climbing is based on pictures of a subject climbing a vertical strip of 6-mm hardware cloth angled 25 degrees from parallel to the line of view (Fig. 6).

A cycle begins with the left hind limb extended and grasping the wire (Fig. 6A). The right hind limb is flexed in a plane parallel to the wire after the foot has released its grip through extension of the phalanges. The claws and basal and distal pads of the thumbs of both forelimbs are in contact with the wire. The right forelimb is slightly flexed and positioned anterior to the head while the left forelimb is strongly flexed and positioned caudad of the head. The left hind limb flexes at the knee and both forelimbs extend, driving the body upward while the right hind limb pulls away from the wire and reaches backward toward a higher grip (Fig. 6B–C). As the hind limbs are nearly side by side, the weight is transferred to both left limbs, and the right forelimb releases contact with a push that swings the body away from the wire (Fig. 6D–F). (This maneuver was noted in nearly all of the motion pictures of climbing and may be the result of avoidance of the wire surface during movements of the limbs. The long, recurved claws of *Desmodus* are better suited for climbing on rough stone than on

screening where they easily become hooked over the wire strands.) The right brachium is pulled caudally and the forearm is flexed, thus lifting the right carpus to the level of the left. As the body is pulled toward the level of the left hind foot and shank, the right hind foot is fully extended and gains purchase on the wire as the right forelimb contacts it (Fig. 6E–G). Although the claws do not actually grasp the wire, the right forelimb provides support through contact of the thumb pads with it. Simultaneous flexion of the shanks of both hind limbs and a cranial and dorsal swing of the thighs lift the body, and the left forelimb releases its grip and is pulled upward by flexion of the elbow and upward rotation of the brachium (Fig. 6H–K). When the left forelimb contacts the wire, the left hind limb is released and extended upward, and the right forelimb is raised, as described for the left forelimb (Fig. 6J–M). Flexion of the right hind limb and extension of the right forelimb lift the body, and the left hind limb is fully extended for a new grip (Fig. 6N). The left forelimb is raised by extension of the elbow to obtain a grip considerably lateral to the climbing path. When the left hind limb grasps the wire and begins flexion to raise the body, the right forelimb is flexed slightly at the elbow (Fig. 6O) to give the thumb a grip higher on the screen. Its thumb is flexed to the level of the distal pad, which rests against the wire. From this position the bat assumes a horizontal resting posture against the wire (Fig. 6P–T).

When vampires descend a vertical surface, the posture and orientation of the body are similar to those seen in climbing, and the movements are also quite similar. Although this behavior was observed on several occasions, it was not photographed for detailed analysis. The bats literally ran down the wire screen on the side of the flight compartment and could stop or change direction almost instantly, indicating sufficient contact of the limbs with the wire to allow control.

Jumping Behavior

The jumping behavior of *Desmodus* is perhaps the most striking and unique feature of its locomotion and is vital to the terrestrial feeding behavior of this genus. Although several other bats can fly from the ground, descriptions of this behavior (Eisentraut, 1936; Orr, 1954; Vaughan, 1959; Altenbach, 1968; Anonymous, 1969)

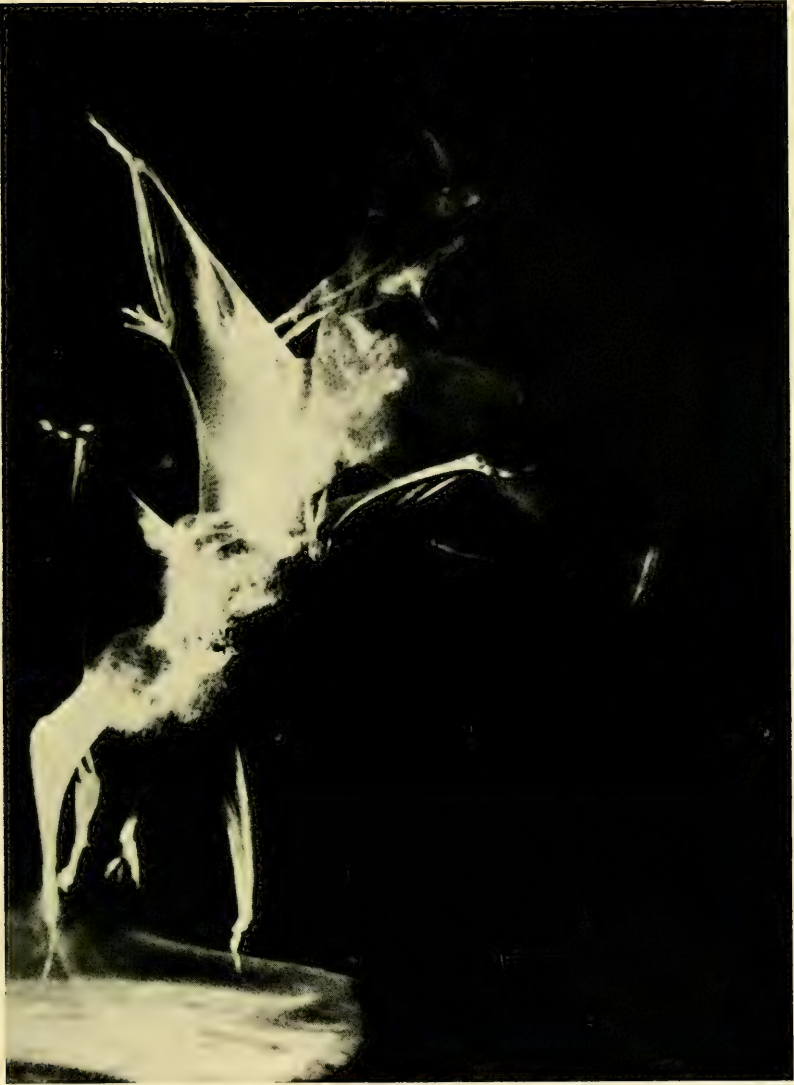


FIG. 7. Multiple exposure photograph of *Desmodus* jumping into flight through an angle of about 60 degrees.

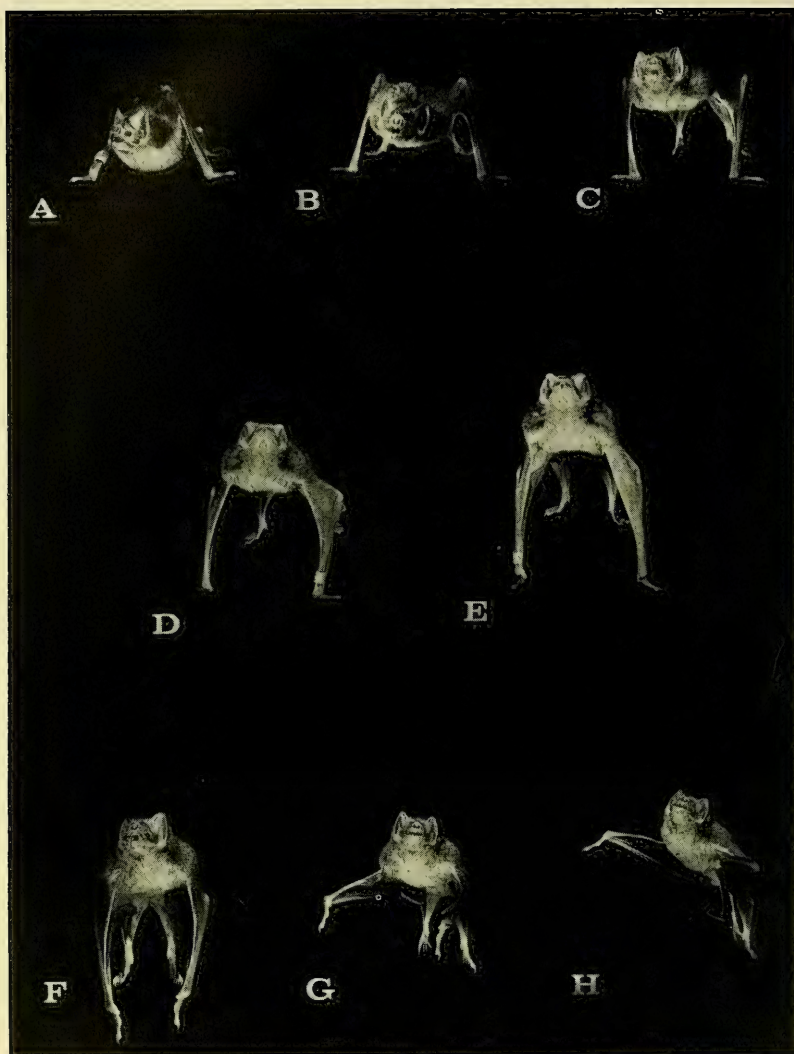


FIG. 8. High-speed photographs of *Desmodus* in the thrusting phase (A-E) and the coasting phase (F-H) of a jump into flight.



FIG. 9. High-speed photographs of *Desmodus* in the last of the coasting phase (I-J) and the initiation of the first downstroke (K) following a jump into flight.

indicate that flight is effected by an adduction of fully or partially extended wings or, on an open surface, by a series of these motions combined with several shallow hops to gain forward speed. Only *Desmodus* launches itself into flight almost vertically from a typical terrestrial stance with folded wings. Several authors (Ditmars and Greenhall, 1935, 1960; Dalquest, 1955; Leen and Novick, 1970) have commented upon the jumping behavior but none has described it in detail nor pointed out its significance.

Recent investigations in México (Robert Tigner, personal communication; Mitchell, 1970) and the observations of Hensel (1869) establish that *Desmodus* does feed from the ground at least occasionally and often moves about on the ground before and after feeding (Ditmars and Greenhall, 1960). Wimsatt (1969) reported that under natural conditions *Desmodus* often consumes more than 50 per cent, and occasionally more than 100 per cent, of its body

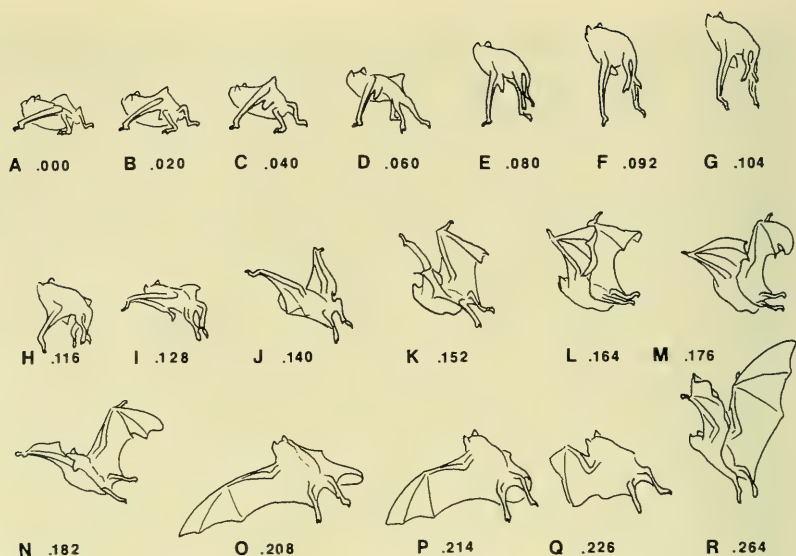


FIG. 10. Drawings of *Desmodus* jumping into flight and corresponding elapsed time in seconds.

weight in blood in a single feeding period. Thus, jumping behavior functions to get a heavily loaded bat into flight from a horizontal surface. In addition, this behavior probably enables the bat to avoid sudden movements of a large host animal that could crush a bat with its foot or to avoid a terrestrial predator such as a snake or carnivorous mammal.

In the laboratory, it was difficult to photograph the bats jumping from an undisturbed walking gait or when startled from a typical terrestrial feeding posture. Thus the majority of the photographic records are of bats suddenly released from beneath a small enclosure. The photographs certainly show typical jumping behavior, especially hurried jumps, which probably are normal in avoidance reactions.

Figure 7 is a multiexposure photograph of a vampire bat jumping into flight through an angle of approximately 60 degrees. It is included to give the reader a better perspective of the directionality and distance involved in a typical jump. The details are described below.

Prior to a jump, *Desmodus* normally crouches with the body close

to the substrate (Figs. 8A, 10A). The brachii are highly abducted and inclined posteriorly five to 10 degrees above horizontal. The elbows are fully flexed, the forearms inclined about 15 degrees anteriorly and slightly laterally, and the thumbs directed laterally with the weight resting on the basal and distal pads. The thighs are abducted roughly 40 degrees above horizontal and directed slightly anterolaterally, laterally, or posterolaterally from the body. The knees are flexed between 90 and 120 degrees and the shanks are inclined posteriorly, posterolaterally, or occasionally posteromedially. The orientation of the hind feet varies between posterior and lateral with the toes slightly spread and the weight resting on the heel pads, the pads at the distal tips of the metatarsals, and the claws. The prejump position is variable, depending upon the nature of the substrate and how rapidly the animal initiates the jump from another posture such as walking or feeding positions. High-speed motion pictures indicate that the bats can jump short distances from nearly any position, but when jumping into flight from a static position on a horizontal surface they usually assume a position similar to that shown in Fig. 8A.

The sequence of movements is highly variable, depending upon the angle of the jump, the plane of the substrate, the orientation of the bat on the substrate, and individual differences. In most of the high-speed photographs of bats jumping into forward flight from a flat, horizontal surface, the jump path was at an angle between 50 and 70 degrees above horizontal. The following description of the movements involved in jumping into forward flight will emphasize this type of jump, which under experimental conditions appears to be the most frequently used. However, *Desmodus* is capable of jumping into flight through angles of 35 degrees to more than 80 degrees. Even in jumps that appear to be nearly identical, careful analysis of motion picture film reveals considerable variation in the magnitude and temporal sequence of the various movements.

The jump is initiated by an inclination of the brachii and resultant declination of the highly flexed forearm (Figs. 8B, 10B–C). This movement shifts the center of gravity at midthorax in a line through the contact of the pectoral limbs and substrate and the direction in which the jump progresses. Extension of the hind limbs, which begins either a few milliseconds before or within 20 milliseconds after the initiation of this movement, aids in the an-

terior shift of the body and supplies upward momentum to the posterior half of the body. As the brachii reach an inclination of between 40 and 55 degrees above horizontal, about 60 milliseconds after initiation of the jump, they are adducted to begin the upward thrust of the jump (Figs. 8B–C, 10C–D). Extension of the elbow normally begins concurrently or within two to five milliseconds after the adduction of the brachium, but if the jump is directed strongly anteriad, extension of the elbow precedes the adduction of the brachium by up to 10 milliseconds and increases the forward shift of the body.

As the hind limbs reach almost full extension, the feet are adducted to provide anterior and upward thrust to the body (Figs. 8C, 10D). Because the center of gravity is positioned over the pectoral limbs in line with the angle of the jump, the last thrust from the hind limbs probably tends to stabilize the position of the body rather than supply much power to the jump.

Adduction of the brachii and extension of the elbows continue about 20 milliseconds and accelerate the bat upward and forward. Although measurement of the movement of parts of the thorax is difficult from photographs of an animal covered with hair, depression of the shoulder joint is evident during adduction of the humerus. This can be partially explained by the humerus being locked dorsally with the lateral scapular border as the lateral scapular border is rocked ventrad, but the depression appears more pronounced than would be accounted for by this movement. The frontal, still photographs of the jump illustrate this best and suggest that depression of the entire shoulder girdle occurs, which necessitates a ventral swing of the distal end of the clavicle (Fig. 8B–E). The depression of the shoulder during adduction of the brachium would add to the upward momentum of the body and thus would certainly be advantageous in jumping. Although no direct evidence is available concerning the exact mechanism of the shoulder depression, analysis of the motion picture films indicates it does occur, and that it begins concurrently with adduction of the brachium and continues through all but the last few degrees of this movement.

Between five and 15 milliseconds before the brachium is fully adducted and the elbow is fully extended, flexion of the thumb begins (Figs. 8D–E, 10E). High-speed photographs show that the thumb remains relatively straight during adduction to provide a lever arm

of maximal length (Figs. 8E, 10E–F). The upward thrust provided by the movements of the body, brachium, and elbow is completed as the thumb leaves the substrate or within a few milliseconds before; thus the thumb provides the last component of thrust in the jump. The contact with the substrate is broken when the thumb is adducted to within about 40 degrees of the long axis of the forearm. After adduction to this point, the forearm is raised almost imperceptibly, and the upward movement of the body facilitates the lift of the thumb off the substrate. Adduction of the thumb continues until it is parallel with the long axis of the forearm. This movement appears to have no function and is probably only a follow-through, as the thumb no longer meets resistance (Figs. 8F, 10G).

Although there is considerable variation among the jumps recorded on motion picture film, the velocity imparted to the body by the jump can readily be measured from the film. The highest velocity recorded as the bat broke contact with the substrate was 2.4 m per second. In 10 other jumps into forward flight, the velocity varied between 1.3 and 2.2 m per second. Although jumping movements are used both in transition from terrestrial stance into flight, and in hopping terrestrial locomotion and avoidance movements, I did not attempt to calculate velocities imparted by jumps except those leading into flight. Simple calculation without consideration of air resistance indicates that an upward velocity of 2.4 m per second will carry an object to a height of about 30 cm. When compared with the motion pictures of the *Desmodus* jumping, this height seemed too great, but the bats normally jumped forward and upward at an angle of between 35 and 70 degrees above horizontal, thus much of the velocity imparted to the body was directed anteriorly.

During the thrust phase of the jump, the long axis of the body is normally inclined upward between five and 20 degrees. The angle appears greater, as the head is often strongly upturned during the jump. The stability of the angle of the body indicates that the weight is effectively centered over the thrusting pectoral limbs and that perhaps the thrust from the pelvic limbs early in the jump counteracts forces that would incline the body.

When the forelimbs leave the substrate, the powered phase is complete and a coasting phase begins with almost immediate flexion of the elbows (Figs. 8F–G, 10G–H). Abduction and supination

of the brachii and flexion of the elbows raise the forearms nearly parallel to a sagittal plane through the body (Figs. 8F–H, 10G–I). As the forearms reach the level of the lower body, extension of the elbows and digits begins (Figs. 8H, 10I). The abduction of the brachii continues, but the supination ceases as the forearms reach the level of the body. Thus the remainder of the wing positioning is a result of abduction and pronation of the brachii and extension of the forearms and digits. Figure 9I–K illustrates the remainder of the coasting phase and the beginning of the first downstroke.

The angle of inclination of the body during this coasting phase of the jump is variable and seems directly related to the flight path during the first few wingbeats. The inclination is often as much as 35 degrees during a coasting phase prior to the first wingbeats of climbing flight. Prior to and during the first wingbeat of nearly horizontal flight, the inclination of the body is reduced to orient the long axis of the body horizontally. This movement is easily explained by the rapid posterior and dorsal movement of the unfolding wings, which imparts a forward and downward force to the anterior body.

The sequence of movements in a more vertical jump is different from those of an anteriorly directed jump. There appears to be little or no inclination of the brachii, and the jump is initiated by adduction of the brachii followed in roughly two to six milliseconds by extension of the elbows. Extension of the hind limbs starts about four to six milliseconds after adduction of the brachii and is directed downward, thus providing little or no forward momentum to the body. The forward thrust that is produced comes from the extension of the elbows, since the brachii are oriented strongly posteriorly during adduction. Adduction of the hind feet is similar to that seen in an anterior jump but provides primarily upward thrust, because the hind limbs are oriented ventrally instead of posteroventrally. Strong flexion of the thumb is initiated prior to the completion of brachial adduction and extension of the elbow to provide the last upward thrust. It appears that a jump forward and upward provides more upward momentum and is better suited to initiating flight from the ground than is a laterally or posteriorly directed jump. A rapid turn made immediately after the jump is usually used in favor of a jump directed laterally.

Lateral and posterior jumps are typically used in avoidance reactions, particularly if the bat is not oriented toward an open flight

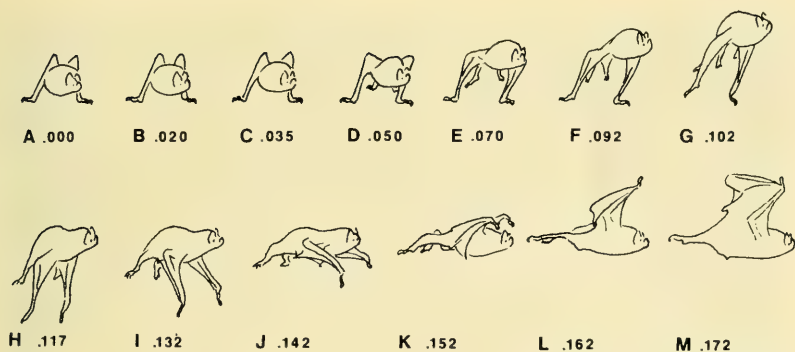


FIG. 11. Drawings of *Desmodus* performing an anterolateral jump and turn into horizontal flight. Numbers are elapsed time in seconds.

path that would allow a forward jump into flight. Most of the lateral and posterior avoidance jumps were recorded only on high-speed still photographs, which prevents detailed description of the movements involved. However, one motion picture sequence of an anterolateral jump was obtained. In this sequence, the hind limbs initially shift the center of gravity slightly forward and laterally into the line of the jump over the pectoral limbs. The major thrust of the hind limbs, however, is almost vertical. Because the body is accelerated laterally, the vertical thrust component of the hind limbs imparts a yaw to the body so that its long axis swings perpendicular to the prejump axis (Fig. 11D–E). The body appears shifted to the left by slight flexion of the left elbow toward the inclined brachium (Fig. 11A–C). Adduction of the right brachium and extension of the right elbow begin and continue to shift the body, and thus the center of gravity, laterad over the left forelimb (Fig. 11D). Adduction of both brachii and extension of the elbows now thrusts the bat upward, slightly forward, and strongly to the left (Fig. 11E–F). The flexion of the right thumb and simultaneous posterior swing of the right forearm swing the long axis of the body toward a position perpendicular to its prejump axis. Flexion of the left thumb supplies the final upward thrust (Fig. 11G). During the coasting phase, the momentum imparted by the right limb swings the body perpendicular to the prejump position (Fig. 11H–M).

A single high-speed photograph of a posterior jump (Fig. 12) indicates that the hind limbs impart slight upward and backward



FIG. 12. High-speed still photograph of *Desmodus* 100 milliseconds after initiation of a posterior jump.

momentum by extension of the knees and adduction of the thighs. The pectoral limbs are probably adducted and extended from the prejump posture with no prior inclination of the brachium, as the extended limbs are seen to be thrust strongly anteriad at the instant of the exposure, about 100 milliseconds after initiation of the jump. It appears improbable that flight could be initiated from a jump of this type, as it did not progress more than a few centimeters vertically and thus would not allow for a full downstroke, although a rolling maneuver could perhaps orient the body in the opposite direction. Jumps such as this are obviously necessary to avoid sudden movements of a host animal, obstacles the host animal brushes by, or predators the bat might encounter on the ground. Flight could readily be initiated after a posterior jump by

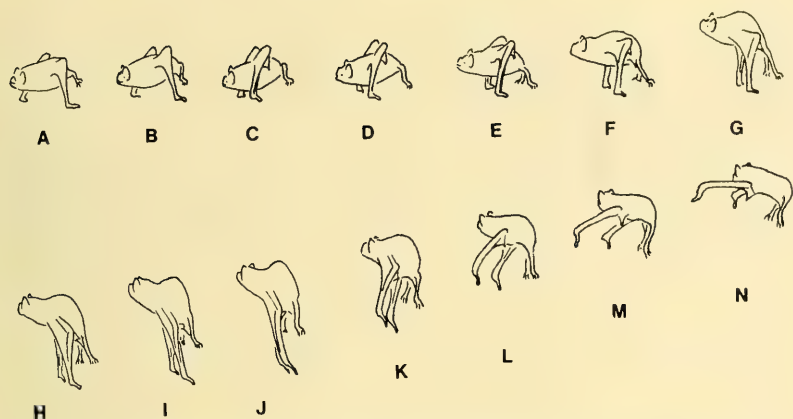


FIG. 13. Drawings of *Desmodus* jumping into flight from a walking gait: A–D, 10 millisecond intervals; D–E, 8 millisecond intervals; E–G, 6 millisecond intervals; G–J, 4 millisecond intervals; J–N, 8 millisecond intervals.

alighting, executing a partial turn, and then jumping anterolaterally or forward.

Figure 13 illustrates a jump into flight following the completion of a stride at a walking gait. As the left forelimb contacts the substrate after a forward swing (Fig. 13A–D), simultaneous brachial adduction and extension of the hind limbs thrust the body forward and upward (Fig. 13E–N). The thumbs supply the final upward thrust typical of jumps initiated from a stationary position.

Desmodus uses the jump to initiate flight from a vertical roosting surface or from the side of a host animal. In the prejump posture on a vertical surface, and brachii are nearly parallel with the long axis of the body, and the forearms are partially extended with the thumbs oriented dorsally and laterally against the surface (Fig. 14A). The hind limbs, which support much of the weight, are held with the knees slightly flexed. The jump is initiated by adduction of the brachii and extension of the forearms with no preliminary inclination of the brachii (Fig. 14B–D). Because the hind feet retain their grip on the surface for a few milliseconds, the thrust of the pectoral limbs sharply inclines the body relative to the vertical surface. The momentum imparted by this movement orients the long axis of the body horizontally in the coasting phase of the jump. As

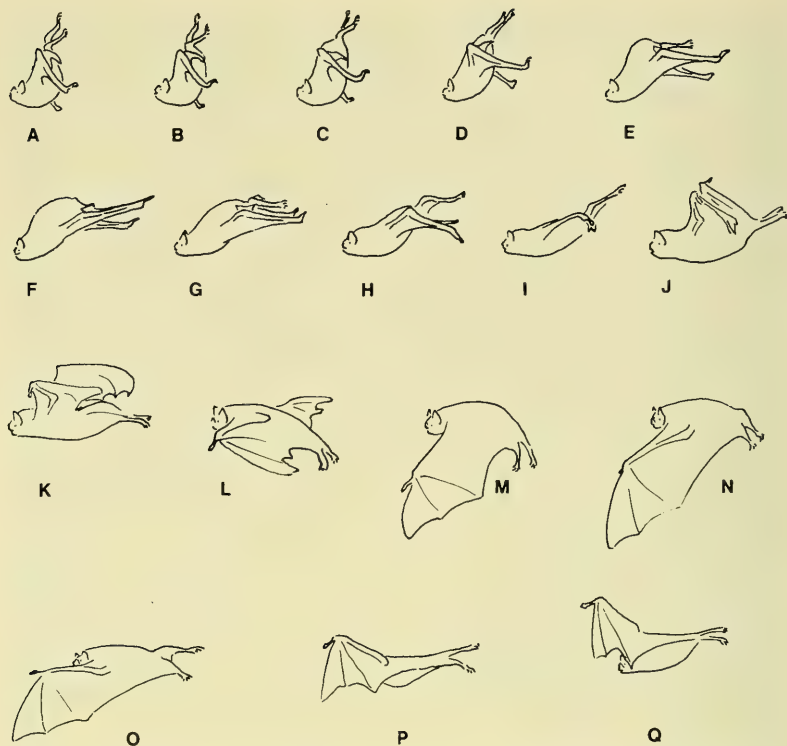


FIG. 14. Drawings at 12 millisecond intervals of *Desmodus* in a jump into flight from a vertical surface.

the adduction of the brachii and extension of the forearms progress, the hind limbs release the surface and the body is thrust laterad and slightly ventrad (Fig. 14D-E). The thrust is completed by extension of the thumbs as in a jump from a horizontal surface (Fig. 14E-F). The elbows remain extended, and the wings are positioned for the downstroke by abduction of the brachii and extension of the digits as the long axis of the body becomes nearly horizontal (Fig. 14G-K). As the airspeed is high because of the lateral thrust of the jump, a downstroke of high amplitude is apparently not necessary and the wings are abducted only 20 degrees above horizontal prior to the first downstroke, which is similar to one seen in level forward flight several wingbeats after a jump from a level surface (Fig. 14L-Q).

Initial Flight Following a Jump

In initial flight following a jump, the position of the body, movements of the wings, and direction of the flight path are variable and, as in other types of locomotion, are dependent upon many factors. A description of the movements recorded on a single high-speed motion picture film would not adequately cover this aspect of locomotion. Still photographs and drawings from films of several different flights will be discussed in an attempt to describe at least most of the characteristics of the flick of *Desmodus*.

When jumping into flight from the ground, *Desmodus* does not have the advantage of species that begin flight from a high roost and can build airspeed by a vertical drop or by a shallow dive during the first few wingbeats (Eisentraut, 1936; Vaughan, 1959, 1970d; Hayward and Davis, 1964; Altenbach, 1968). Although some other bats can take flight at a steep angle from a horizontal surface, the majority of these have light wing loading or complex modifications of the wingbeat cycle that allow hovering. *Desmodus* is heavily loaded (Struhsaker, 1961; Hartman, 1953), and my investigation revealed no extreme wingbeat modifications typical of heavy-bodied, hovering species (Altenbach, 1968). The only forward airspeed available to *Desmodus* after a jump is provided by the momentum of the jump.

During photography of jumps into flight, bats normally did not fly higher than 0.3 to 0.6 m above the level of the surface from which they jumped. Thus the flight path was usually inclined no more than 15 degrees above horizontal, although in a few instances bats flew upward at an angle of 60 or 70 degrees above horizontal. When released on the laboratory floor, *Desmodus* typically jumped from the floor and flew within less than a meter of it for as far as 10 m. Dalquest (1955) and Wimsatt (1959) commented that *Desmodus* flies within a meter of the ground.

Coasting phase and initial flick.—In a jump into a forward flight with a climb path of five to 10 degrees (Fig. 15), the body is slightly inclined during the coasting phase. As the wings are abducted to the level of the body (Fig. 15G–I), within about 100 milliseconds of initiation of the jump (Fig. 15I), the forward motion imparted by the jump is only about 0.2 m per second. However, as the forearms and digits are extended and the wings are abducted, the distal half of the wings assumes a configuration that provides for-

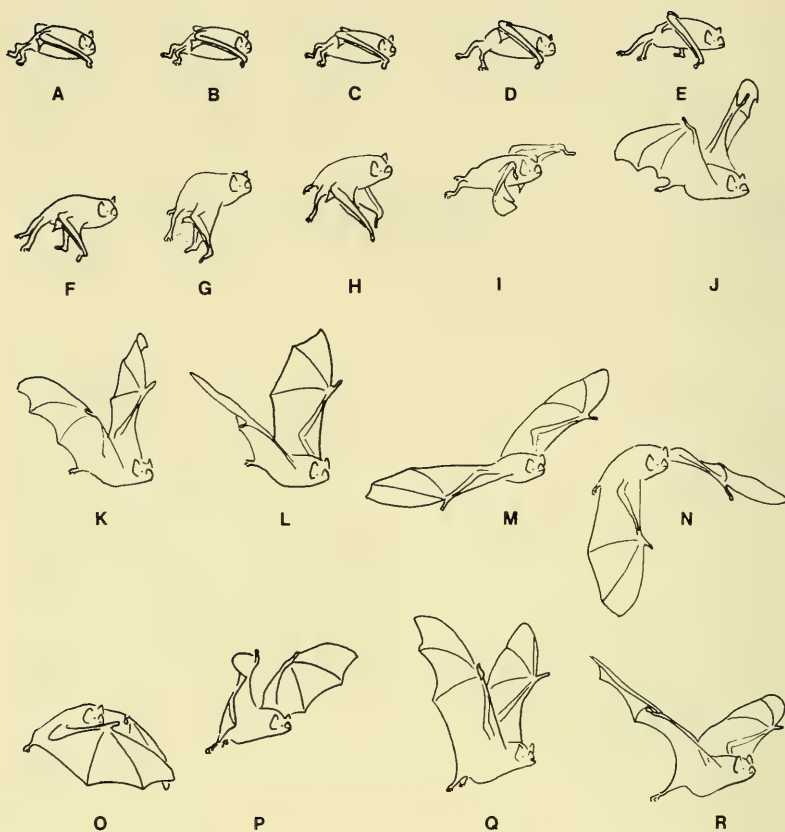


FIG. 15. Drawings at 20 millisecond intervals of *Desmodus* in a jump into nearly horizontal flight.

ward thrust (Fig. 15I-J). As extension of the wings begins, the digits are inclined posteroventrally between 60 and 80 degrees below horizontal. In the next 30 milliseconds, the digits are fully extended and inclined posteriorly through an arc of roughly 70 degrees, as the wings are raised 50 to 60 degrees. The movement of the distal half of the wings is rather complex and is the result of several movements of the arms and hands. Extension of the digits and extension of the forearms impart a rapid lateral movement to the wingtip. Abduction of the arm adds a vertical com-

ponent to this movement, and pronation of the arm and extension of the phalanges add a posterior component. Through the first half of this movement, while the digits are still directed strongly ventrally, the distal half of the chiropatagium attains velocities of 11 to 12 m per second. During this phase, the average forward velocity of the bat increased from 0.2 m per second to 0.56 m per second, indicating that forward thrust was being produced. In descriptions of forward and hovering flight in other species of bats, Eisentraut (1936) and Norberg (1970a) indicated that, in the last phase of the upstroke, similar movements produce strong forward thrust.

As the wing reaches a fully abducted position prior to the initiation of the downstroke (Fig. 15J–K), decreased velocity at the distal chiropatagium probably reduces forward thrust.

First downstroke.—The transition from upstroke to downstroke is not clearcut, but is marked by a progressive change in the direction of movement. At peak upstroke the wings are positioned about 60 degrees above horizontal and full extension of the digits has oriented the distal plagiopatagium and all but the trailing edge of the chiropatagium almost behind the leading edge (Fig. 15K). The terminal phalanges of digits III, IV, and V still are slightly flexed ventrally from the dorsal air pressure during abduction, thus the trailing edge of the chiropatagium is below the plane of the rest of the wing. The hind limbs are fully extended posterior to the body and parallel with its long axis.

The downstroke begins with a slight anterior swing of the brachii (Fig. 15L) accompanied by adduction and pronation of the arms. This movement depresses the leading edge of the wings and eliminates the ventral flexion of digits IV and V. Eisentraut (1936) maintained that complete extension of the phalanges of digits IV and V is the result of air pressure against the membrane adjacent to them. However, analysis of several high-speed motion picture films of the start of the downstroke leads me to believe that, although adduction of the wing is evident and air pressure from below contributes to this movement, an active dorsal extension of the digits also is involved. The movement of the wing is slight as the phalanges are rapidly extended. There appears to be no pronounced dorsal billowing of the chiropatagium between digits III, IV, and V as would be expected if the force of the air were causing the movement of the phalanges. As adduction of the wings pro-

gresses ventrally and slightly anteriorly, the arms remain strongly pronated. The pronation and the force against the air below the wings cause the trailing edges of the distal half of the plagiopatagium and the chiropatagium to be about 10 degrees above the leading edges (Fig. 15L-M). This portion of the wings is thus in a thrusting configuration, as the air is readily accelerated posteriorly to impart a forward component of force to the wing, as described by Eisentraut (1936) for this phase of the wingbeat in forward flight of other bats. The leading edge of the chiropatagium, or digits II and III, is depressed relatively more than the membranous propatagium because of the strong pronation of the brachium. Even when the limb is in a fully extended position, the long axis of the forearm is angled between 30 and 40 degrees ahead of the axis of the brachium; thus pronation of the brachium imparts a ventral swing to the distal forearm and anterior digits (Fig. 15M). Air pressure tends to bend the phalanges of digit IV dorsad thus adding to the thrusting configuration of the wing. The dorsal bending of the fourth digit to produce the thrusting of the distal chiropatagium is described by Vaughan (1959, 1970*d*, 1970*e*), who estimated that in the species of bats he studied no more than 20 per cent of the wing produced thrust during any phase of the wingbeat cycle (Vaughan, 1970*d*). It is evident from analysis of the motion pictures of *Desmodus* in flight that probably 60 to 80 per cent of the wing provides thrust. This thrust is greater distally than proximally because of the greater angle of anteroventral inclination of the chiropatagium and the more rapid movement of the wing distally. The extremely large part of the wing producing thrust is probably necessitated by the high wing loading in this species coupled with the habit of taking off from the ground where high thrust is vital to gain sufficient airspeed for more efficient flight.

The hind limbs are depressed concurrently with, or slightly later than, the adduction of the brachii and thus depress the trailing edge of the plagiopatagium, which in turn shapes the medial half to one quarter of the plagiopatagium into a more cambered surface than at the start of the downstroke.

Superimposition of successive motion picture frames of the coasting phase of a jump and the first wingbeat indicates that, prior to the beginning of the downstroke, the upward velocity has dropped to about 0.3 m per second although the forward speed

has been increased by the flick phase of the upstroke. By the end of the first half of the downstroke, upward velocity of the body increases to an average of 0.5 m per second indicating production of lift. Forward velocity also increases, indicating production of thrust during the downstroke. The magnitude of this acceleration was not calculated because the bat was flying toward the camera. Direct observation of the motion pictures projected at 16 frames per second shows a definite upward "hop" of the bat during the first downstroke. The amplitude of the hop varied between different films but was as great as 12 mm during the first half of the stroke. This hop is equally evident in flights where the forward speed at the start of the downstroke was extremely low (about 0.1 m per second). It seems obvious that an upward and forward acceleration of the bat results from a downward and backward acceleration of air as the wings are swept through the downstroke.

From the level of the body, the path of the downstroke becomes increasingly more anterior. The arms remain strongly pronated as the wings are adducted past the level of the body, but as they reach an angle of approximately 30 degrees below a horizontal plane through midbody, the pronation is lessened (Fig. 15N). The upward bending of the phalanges of digit IV continues, although the anteroventral inclination of the leading edge is reduced. The upward deflection of digit V is eliminated by flexion of the phalanges, thus increasing supination of the wing, and continuous depression of the hind limbs depresses the trailing edge of the entire plagioptagium below the leading edge of the wing. Air acceleration during this phase of the stroke would be strongly downward and would supply a component of high lift.

As the wings reach an angle of roughly 50 degrees below horizontal, the adduction of the brachii is almost stopped and a flexion of the forearms and pronounced supination of the arms begin (Fig. 15N–O). This movement strongly supinates the distal half of the wings and swings them anteriad and mediad. The air acceleration from the more medial portions of the wing is directed somewhat downward by these movements thus producing more lift and thrust while air acceleration from the chiropatagium still produces thrust.

Upstroke and flick.—There is no sudden transition into the upstroke, rather a uniform transition to a different direction of movement. As the opposing planes of chiropatagii become parallel, con-

tinuing flexion of the forearms and supination of the brachii lift them vertically in this position (Fig. 15O) toward the level of the body. The digits remain fully extended during this movement and the vertical orientation of the entire chiropatagium and much of the distal plagiopatagium keeps the air resistance to this movement minimal.

Abduction of the brachii begins with the vertical movement of the forearms and occurs simultaneously with abduction of the hind limbs. The elastic properties of the plagiopatagium, and perhaps also contraction of the *M. coraco-cutaneous*, appear to reduce its size when the wings are in an anterior position and probably help to reduce drag. The hind limbs maintain tension posteriorly to stretch the membrane and prevent it from flapping from the forward motion of the body. Since the bat is rapidly accelerating during the first few wingbeats, reduction of drag is vital.

There is considerable flexion of the phalanges of digits III, IV, and V during this phase of the stroke, probably the result of sudden loss of pressure against the ventral surface of the chiropatagium and distal plagiopatagium while this membrane is raised vertically. Considerable flexion of the digits (metacarpals) toward the forearm also occurs during the last phase of this part of the stroke. Flexion of the phalanges at this stage is of functional importance since their extension during the next stage provides increased thrust.

As abduction and supination of the brachii raise the carpi above the level of the body, extension of the forearms begins. Extension of the forearms and digits and abduction of the brachii swing the chiropatagii first laterally and then posterodorsally (Fig. 15P). The posterodorsal swing is exaggerated by a pronation of the brachii when they reach their highest angle of inclination (Fig. 15Q). This is the thrusting phase described in the upstroke of other species of bats by Eisentraut (1936) and Norberg (1970a), who termed it the "flick phase." As the chiropatagium is extended, supinated, and abducted from a vertically oriented position anterior to the head, its movement against the airstream imparts a large component of forward thrust to the wings.

There is extreme variation in the first wingbeat cycle, and the above description pertains only to flight that is nearly horizontal. Frequently the digits are not fully extended at the beginning of the downstroke and the phalanges of digit III remain flexed at the



FIG. 16. Drawings at 15 millisecond intervals of *Desmodus* in a jump into flight with the digits not fully extended.

TABLE 1

RELATIVE LENGTHS OF TIME (IN SECONDS) OF PHASES OF WINGBEAT CYCLES OF *Desmodus rotundus* FOLLOWING A JUMP INTO FLIGHT IN FIVE TRIALS OF INDIVIDUALS. ABBREVIATIONS: I, INITIAL FLICK; D, DOWNSTROKE; U, UPSTROKE PRIOR TO FLICK; F, FLICK.

Wingbeat number	Phase	Trial number				
		1	2	3	4	5
1	I	.030	.048	.036	.040	.038
	D	.052	.040	.048	.048	.052
	U	.020	.020	.024	.024	.024
	F	.018	.022	.024	.018	.028
2	D	.048	.054	.050	.048	.056
	U	.014	.028	.026	.026	.022
	F	.022	.016	.020	.018	.018
3	D	.052	.058	.052	.050	.050
	U	.014	.020		.020	.018
	F	.026	.018		.018	.020
4	D	.058				
	U	.020				
	F	.024				

second and third interphalangeal joints. This illustrates the importance of the thrust produced by the medial chiropatagium and distal plagiopatagium as the leading edge of the wing is declined below the trailing edge. The view that thrust is produced only by the propeller configuration of the distal chiropatagium between digits III and IV as the phalanges of digit IV bend upward obviously does not apply to the initial flight of *Desmodus*. Figure 16 illustrates this in a bat jumping into a flight path that is inclined upward about 10 degrees. The upward and forward momentum imparted by the jump was low and the bat initiated flight with an air speed of about 0.2 m per second. The first downstroke starts with the digits partially extended from the forearm and the phalanges of both third digits flexed in a configuration typical of a folded wing (Fig. 16I). Because the bat is flying toward the camera, the forward speed is nearly impossible to calculate without complex photogrammetric procedures. However, forward acceleration was reflected in the increasing size of the image of the bat on the film. The drawings in Fig. 16 all are to the same scale and do not reflect increasing size of the photographic images. The digits are not fully extended until the last of the third wingbeat cycle (Fig. 16CC), yet

prior forward acceleration (Fig. 16G–CC) indicates thrust was produced. The propeller configuration of the chiropatagium noted above, and described earlier by Vaughan (1959), was certainly not possible, thus thrust was probably produced by the distal portion of the plagiopatagium and the proximal portion of the chiropatagium during the downstrokes. No doubt the initial flick and the flicks in the subsequent wingbeat cycles produced additional thrust.

Time periods for the initial flick and for portions of initial wingbeat cycles in several flights are presented in Table 1. Although there is considerable variation between flights, it is evident that the initial flick, because of its greater amplitude, lasts longer than subsequent flicks and provides thrust over a longer period. The upstrokes (including the flick) require less time than the downstrokes, as Eisentraut (1936) described for other species, and reflect the low resistance of the wing against the air stream initially, and the rapidity of the flick.

Steeply inclined flight and turning maneuvers.—If the flight path is inclined steeply upward or if the bat executes a relatively sharp turn during the first few wingbeats after a jump, the angle of the long axis of the body is usually steeply inclined during the coasting phase of the jump and initial wingbeats. Figure 17 illustrates a jump from an inclined surface and an immediate right turn into nearly level flight. Both upward and forward velocities were low (about 0.2 m per second) at the start of the initial flick. The body is inclined upward at about 60 degrees during the coasting phase of the jump and remains in this attitude during the entire turn. The flick progresses as described above, but the inclination of the body directs more of the air acceleration downward thus providing both upward and forward acceleration to the body (Fig. 17I–K). The downstroke is similar to the one described above and is characterized by strong pronation that orients the leading edge of the wing approximately 20 degrees below the trailing edge over the distal two-thirds of the plagiopatagium and entire chiropatagium. The inclination of the body directs much of the air acceleration downward, thus supplying high lift and upward momentum. The downstroke progresses far ventrally, relative to the bat, apparently to provide air acceleration for a relatively longer time than in horizontal flight after a jump (Fig. 17L–M). The bat has jumped into a virtual stall and needs all possible downward air acceleration to remain airborne. The turn is initiated at the flick phase of this

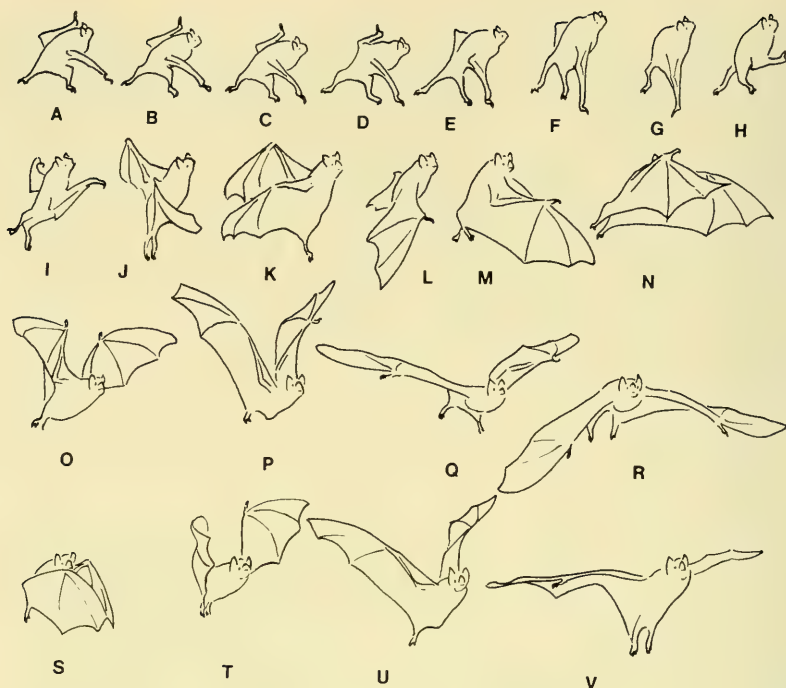


FIG. 17. Drawings at 20 millisecond intervals of *Desmodus* in a jump into steeply inclined initial flight.

wingbeat, but the unilateral differences that effect the turn are subtle. In another series of drawings of a turn following a jump, the right hind limb is depressed far below the left early in the first two downstrokes (Fig. 18I-J, 18O-P). This provides greater drag on the right side of the body as well as reduced thrust resulting from reduction of the area of the wing oriented to provide thrust. The resultant differences in forward velocity of the wings apparently produce a right turn. The upstroke effects a horizontal orientation of the body, and the flight progresses horizontally at nearly a right angle to the direction of the jump (Fig. 18R-U).

In flight inclined at greater angles, the wing movements are similar but the inclination of the body is greater. High amplitude downstrokes occur at about the same angle relative to the bat, but the resultant air acceleration is directed downward to provide upward momentum.

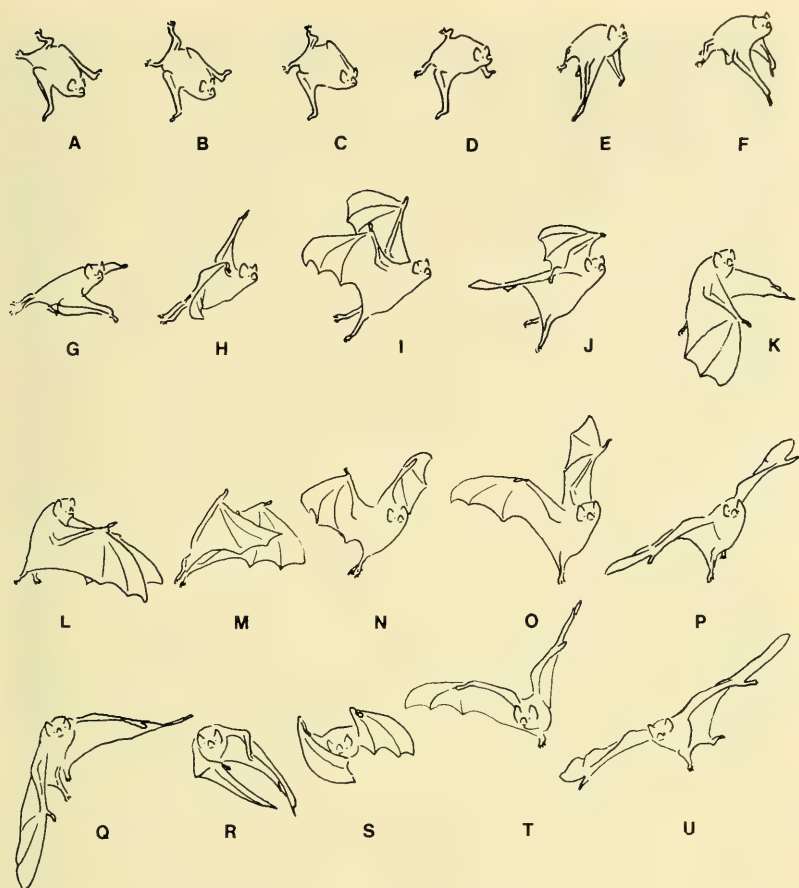


FIG. 18. Drawings at 20 millisecond intervals of *Desmodus* in a jump into flight followed by a turn during the first two wingbeats.

Slow Forward Flight

High-speed still photographs (Figs. 19, 20) taken from the side, about four to eight wingbeats after a jump into horizontal flight, illustrate changes that occur in the wingbeat cycle and show rather subtle features of the wings that are not apparent in the motion pictures. This series of pictures was selected from nearly 300 still photographs of flight sequences of different individuals to best illustrate particular features of the wingbeat cycle.

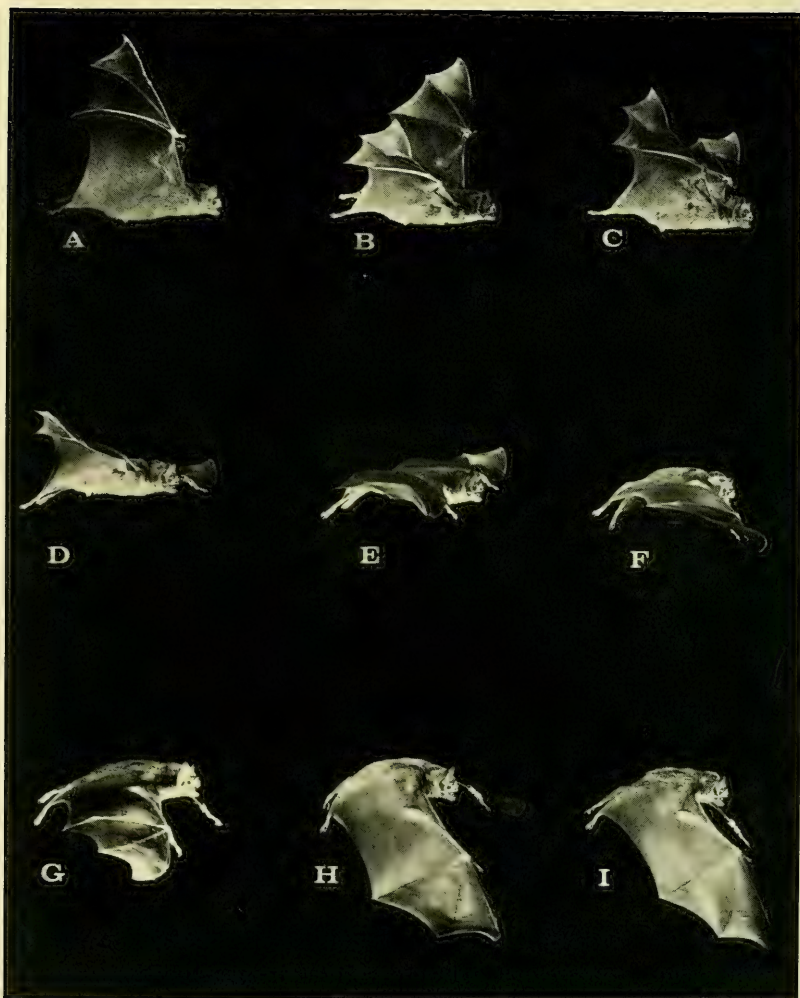


FIG. 19. High-speed still photographs of stages in the downstroke of *Desmodus* in slow, forward flight.

After the first four to eight wingbeats in level flight the bat has accelerated to about 2 m per second and its aerodynamic requirements have changed somewhat from those in the wingbeats immediately following a jump into flight. The bat is still accelerating to a flight speed that is typically over 5 m per second and the

wingbeat must still produce lift and thrust. However, the bat has the advantage of air speed that will allow the deflection of air by the wings as the bat passes through it.

Downstroke.—At the start of the downstroke the strong pronation characteristic of the beginning of adduction is evident (Fig. 19A). As the downstroke progresses, pronation of the entire arm is evident, and an upward deflection of the terminal two bony phalanges of digit III and the phalanges of digits IV and V can be seen (Fig. 19B–C). This upward deflection is the result of the upward pressure of air as the wing is adducted and perhaps contraction of the phalangeal extensors as well. The deflection is most obvious in digits III and IV (about 30 degrees above the long axis of the metacarpals) and only slight in digit V (about eight degrees above the long axis of metacarpal V). The upward deflection of the phalanges of digit V appears unique and has not been described for any other bat. This configuration increases the posterodorsal inclination of the medial wing and, along with the upward billowing of the distal half of the plagiopatagium, produces a thrusting surface for this part of the wing. The upward deflection of digit IV is typical of all bats during the downstroke, and serves primarily to increase the upward inclination of the chiropatagium between digits III and IV to provide a high thrust component, as this part of the wing is adducted at a higher velocity than the more medial parts of the wing. The upward inclination of the phalanges of digit III is more difficult to explain functionally. It reduces the forward thrusting capabilities of the distalmost part of the wing and directs forces on the membrane between the phalanges of digits III and IV medially, rather than anteriorly, as exhibited in other species of bats (Eisentraut, 1936; Vaughan, 1959, 1970*d*, 1970*e*; Altenbach, 1968). Due to the posterior curve of the distal part of the leading edge of the chiropatagium and the strong pronation of the arm, low resolution photographs of the bat flying toward the camera do not show this condition, although it may be present. Although this configuration of the distal wing is perhaps important in providing lift later in the downstroke, it may function at this stage to alter the tip vortex. The bat has an air speed of about 2 m per second at this time, and certainly tip vortices could alter airflow characteristics across more medial parts of the wing. *Desmodus* has an extremely high wing loading and does not have a long wing to displace the tip vortices distally as do some of the

equally heavily loaded molossid bats, such as *Eumops perotis* and *Tadarida molossa* (Vaughan, 1959, 1966), and *Molossus ater* (Hartman, 1963). Other means of reducing the vortices may be essential in *Desmodus*. Photographic evidence for heavily loaded, low aspect ratio bats like *Artibeus jamaicensis* would be interesting to analyze to see if this phenomenon also occurs in them.

As the wing is adducted to the level of the body, the dorsal deflection of phalanges of digit V is first reduced and then eliminated by ventral flexion (Fig. 19D-E). Adduction of the hind leg during this stage depresses the trailing edge of the plagiopatagium and increases the camber to deflect and accelerate air downward to provide an increasing component of lift (Fig. 19D-F). As the wing is adducted below the body (Fig. 19F-G), flexion of the phalanges of digit V becomes more pronounced and, along with continued adduction of the hind limbs, increases the camber and angle of attack of the entire plagiopatagium and medial half of the chiropatagium between digits IV and V. The phalanges of digits IV and III remain deflected upward to maintain the thrusting configuration of the lateral chiropatagium between the phalanges of digits V and IV, and of all the surface between the phalanges of digits III and IV. As the stroke progresses antieriad and ventrad, the configuration of the lateral chiropatagium that produces posterior air acceleration and thrust in the middle of the downstroke now produces increasing lift generation from this portion of the wing (Fig. 19H-I).

Upstroke and flick.—The flexion of the forearms approximates the distal plagiopatagii and chiropatagii as described in initial flight, and supination and abduction of the brachii raise the forearms, and thus the vertically oriented wings, parallel and anterior to the body (Fig. 20J-L). The smooth transition from downstroke to upstroke by an anterior and medial movement of the wings is important for two reasons. First, this type of transition allows for a wing configuration that permits a thrust and lift generating movement during the upstroke. Second, the waste of muscular effort to reverse direction of movement is reduced by a transition involving only gradual change of configuration and direction of movement. At the level of the upper body, flexion of the digits is noticeable (Fig. 20M), and the flick phase is initiated by extension of the forearm and digits, and by abduction and pronation of the arm at the brachium (Fig. 20N-O). The phalanges of digits III,

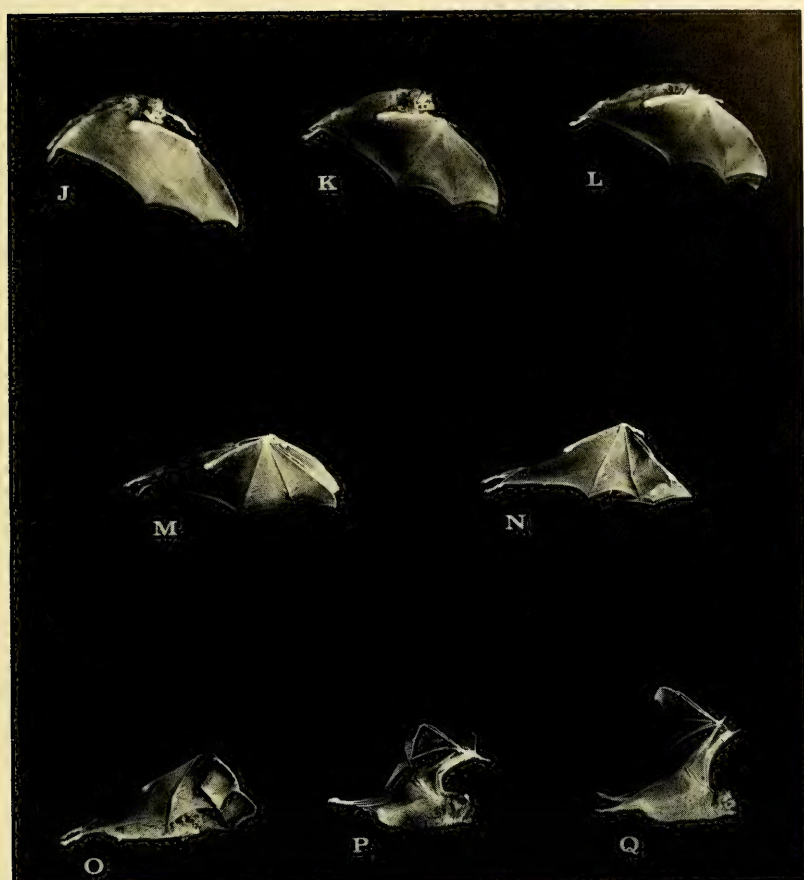


FIG. 20. High-speed still photographs of stages in the upstroke and flick of *Desmodus* in slow, forward flight.

IV, and V remain ventrally flexed during this rapid movement and help maintain an efficient thrusting surface. Although Eisen-
traut (1936) described this flick phase in detail and suggested it
provided a strong forward thrust, it has not been credited with
providing thrust by more recent investigators of bat flight. Most
other descriptions of bat flight, except that of Eisen-
traut (1936), imply that the upstroke in bats is typically a recovery stroke, as it
is in most birds (Storer, 1948), and provides no forward thrust.
The strongest evidence that the flick phase actually produces thrust

is the acceleration seen during the flick phase prior to the initial downstroke after a jump into flight described earlier. The still photographs illustrate the ventral and anterior billowing of the chiropatagium between digits III, IV, and V (Fig. 20O) as the chiropatagium swings laterad, posteriad, and dorsad. Similar billowing of the plagiopatagium immediately medial to digit V of the chiropatagium and between the phalanges of digits V, IV, and III is evident in Fig. 20P-Q, indicating that an anterior force is generated here by the pressure of the airstream. The billowing of the patagii anteriorly, the rapidity of the movements of the flick phase, and the acceleration evident during a similar movement after a jump provide convincing evidence that considerable forward thrust is produced.

Motion picture data on slow forward flight.—A series of drawings from motion picture film taken of the third and the beginning of the fourth wingbeat after a jump into horizontal flight further illustrates some of the features considered previously (Fig. 21). The pronation at the first of the downstroke is seen at A and B. The leading edge of the wing at the level of digit V is depressed fully 15 degrees below the trailing edge. Although not visible, the phalanges of digit V are probably deflected upward, because the upward deflection of the phalanges of digits III (second and third phalanges), and IV can readily be seen in the right wing (Fig. 21B). As the wing is adducted, the effect is no longer obvious, illustrating that the angle of the wing relative to the camera can easily obstruct the view of critical details of the flight mechanism. In Fig. 21D-H, the adduction is clearly seen as is a decrease in pronation and increase in medial camber accompanying depression of the hind limbs during the last half of the downstroke. Flexion of the forearms (Fig. 21G-I) brings the wing medially and strongly anteriorly. The flick phase is initiated at Fig. 21J and terminates about 22 milliseconds later between M and N. Fig. 21N-Q shows the beginning of adduction and pronation of the wing and establishment of the upward deflection of the phalanges of digits III and IV.

Although they do not show the upward deflection of the phalanges of digit V, drawings of frames of motion picture film taken from the side of a bat in forward, horizontal flight at about 2.5 m per second show the upward deflection of the phalanges of digits III and IV, the purely ventral movement of the strongly pronated wing to the level of the body, and the decrease in pronation after

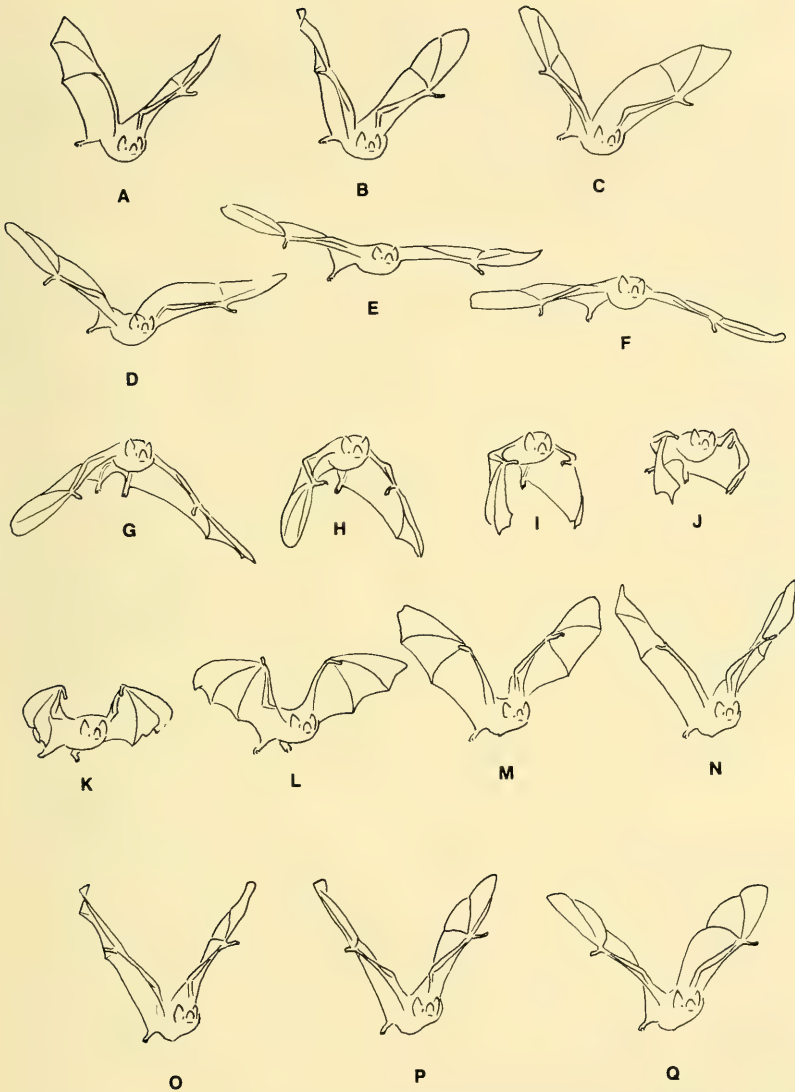


FIG. 21. Drawings of a head-on view of *Desmodus* in slow forward flight. Time intervals (milliseconds) between successive positions are: A-B, 6; B-C, 12; C-D, 8; D-E, 8; E-F, 8; F-G, 10; G-H, 8; H-I, 6; I-J, 6; J-K, 8; K-L, 6; L-M, 6; M-N, 4; N-O, 2; O-P, 2; P-Q, 6.

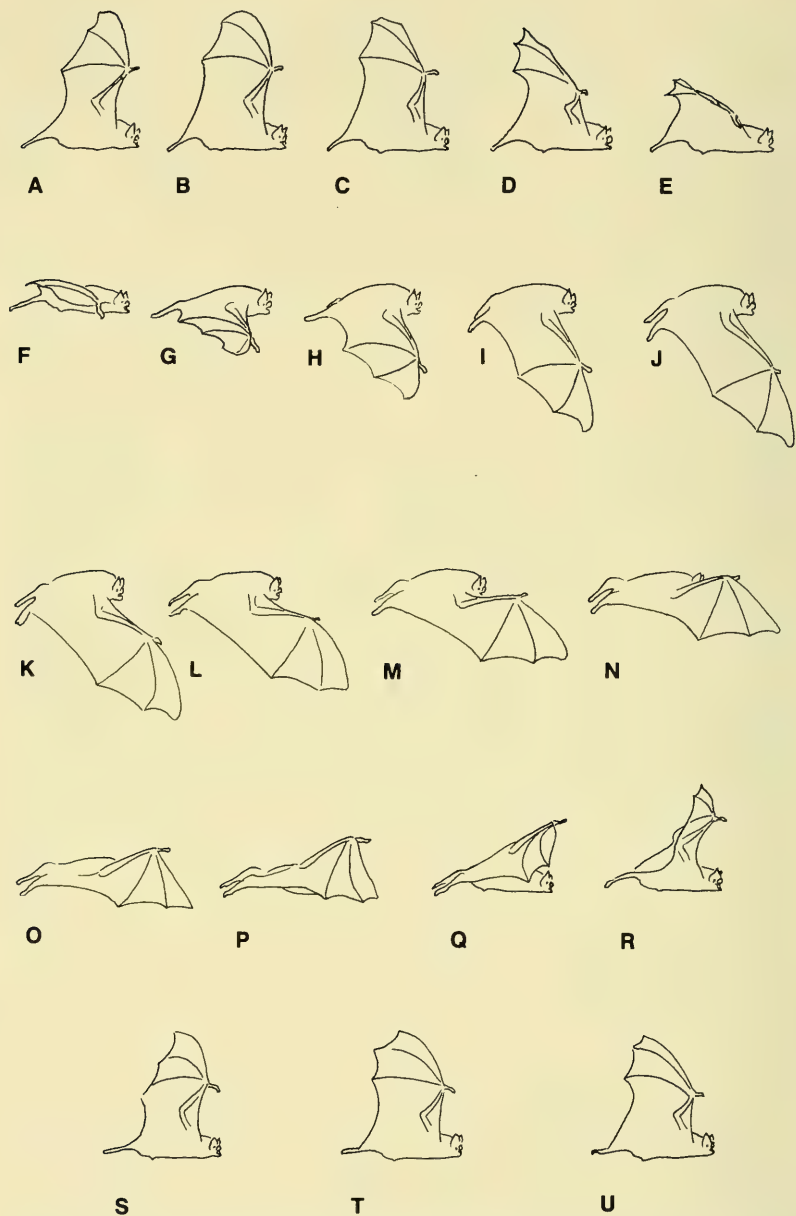


FIG. 22. Drawings at 5 millisecond intervals of a side view of *Desmodus* in slow, forward flight.

that point (Fig. 22A–G). It is certainly possible that at this airspeed, the upward deflection of the phalanges of digit V may be obliterated or prevented in the early downstroke by phalangeal flexors. Sufficient thrust may be generated by posterior air acceleration from more distal parts of the wing, and it may be advantageous to maintain a cambered medial wing to deflect air downward and produce lift. In the last part of the downstroke, the wing is oriented more anteriorly and adducted to about 70 degrees below horizontal. The deep amplitude of the downstroke seems characteristic of slow, stable, accelerating flight and is probably an effort to get as much forward thrust and lift as possible from the downstroke. The initiation of the upstroke begins with flexion of the strongly adducted forearm, which raises the vertically oriented distal segment of the wing. Abduction and supination of the brachium begin relatively later than in the initial few wingbeats, perhaps to delay the flick phase until the wing is slightly above the level of the body. Early initiation of the flick phase from a ventral position would necessitate the abduction of the plagiopatagium in a relatively horizontal position over a fairly wide arc, and thus would require considerable energy. When the flick phase is delayed until the wing is above the body, the plagiopatagium is raised to the level of the body in an anteriorly oriented, stretched, low drag configuration (Fig. 22K–O). During the flick phase, the lateral plagiopatagium produces thrust along with the chiropatagium (Fig. 22P–S). As flight speed increases, the flick probably plays a lesser role in thrust generation.

Alighting Maneuvers on Horizontal Surfaces

As *Desmodus* is so highly terrestrially oriented in feeding behavior, the transition between flight and terrestrial locomotion on a horizontal surface is an important aspect of its locomotor behavior. Again, the maneuvers in this phase of locomotion are quite different depending upon differences in the flight prior to alighting, the contour of the surface, and, no doubt, individual differences. Tracings from a high-speed motion picture film of a bat alighting from slow, almost hovering flight (about 0.2 m per second), show that as the wings are in position for a downstroke, there is a strong anterior movement of the forearms by an anterior swing of the brachii and flexion of the elbows (Fig. 23A–B). The forearms,

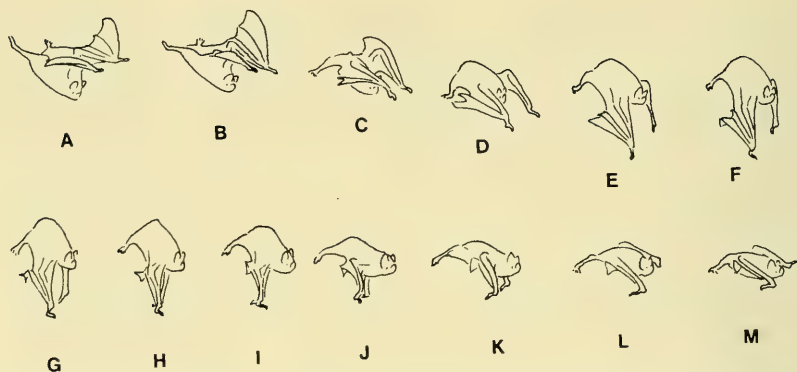


FIG. 23. Drawings at 10 millisecond intervals of *Desmodus* alighting on a horizontal surface.

oriented parallel to the long axis of the body, which is inclined anteriorly, are lowered by adduction of the brachii to the level of the body (Fig. 23B-D), and the digits are folded toward the configuration seen in terrestrial locomotion. Strong flexion occurs at the joints between phalanges two, three, and four of digit III, and between phalanges one and two of digits IV and V. As the brachii are adducted below the middle of the body, pronounced extension of the elbows begins (Fig. 23D-E). Adduction and an anterior swing of the brachii orient the forelimbs almost vertically beneath the shoulders. Prior to contact with the substrate, the thumbs are nearly in line with the long axis of the forearms (Fig. 23E). As the thumbs contact the substrate, they bend upward at the metacarpophalangeal joints to begin absorption of the impact. A posterior swing and abduction of the brachii shift the center of gravity anteriorly over the forelimbs and, in combination with flexion of the elbows, begin to break the fall (Fig. 23F-I). Dorsolateral bending of the first metacarpals lowers the carpi to the substrate during these movements and also probably helps break the fall. The body remains inclined anteriorly below horizontal, but the hind limbs are flexed at the knees and adducted posterolaterally to accommodate the ventral pull of the plagiopatagii. As the brachii are abducted to the level of midbody, the inclination of the body is reduced, thus dropping the hind limbs toward the substrate (Fig. 23H-L). The folding of digits of the forelimbs is complete before

the hind limbs contact the substrate (Fig. 23L). Nearly all of the shock of the landing is absorbed by the pectoral limbs, and the hind limbs appear to absorb little of the energy.

Many parts of the fall-breaking maneuver are similar to the movements seen in a jump, although the direction of movement is reversed. No electromyographic data are available, but no doubt the muscles that power the jump supply force to break a fall in a sequential series of contractions. The pelvic limbs play an even lesser role in alighting on a horizontal surface than during a jump.

When released in confined and unfamiliar surroundings, *Desmodus* often lands on the floor with a solid "plop," indicative of little or no breaking of the fall. However, when accustomed to the surroundings, as in a large flight cage or in a roost, the alighting is delicate and almost noiseless. I assume that, when alighting on a horizontal surface from flight, the breaking maneuver of the pectoral limbs is used consistently. This behavior is of obvious advantage to avoid internal injuries from a hard fall, and perhaps to lessen the noise of alighting when intending to feed on a host animal from the ground or to lessen the impact when alighting directly on the animal. Because my observations and those of others indicate that *Desmodus* often flies close to the ground (Wimsatt, 1959), a simple stalling or braking maneuver could cut air speed and allow a short drop to the ground that would not necessitate strong breaking of a fall.

Alighting Maneuvers on Vertical Surfaces

When alighting on a vertical surface from forward flight, *Desmodus* characteristically executes a steep bank during the flick phase of the upstroke and brakes with a shallow downstroke. As the bat slows, its digits are rapidly flexed toward the forearm and the phalanges of digits III, IV, and V are flexed ventrally. The forelimbs and hind limbs appear to contact the surface simultaneously in a spread position, as described by Eisentraut (1936) for *Myotis myotis*. In *Desmodus*, the hind limbs are flexed at the knee and oriented posterolaterally. The forelimbs are only slightly flexed at the elbow, and the thumbs are directed laterally. Immediately upon alighting, the bat turns head down by alternate flexion of the hind limbs, and hangs in the characteristic posture with the hind legs flexed at the knee and the forelimbs slightly flexed and

oriented laterally. The thumbs are directed dorsolaterally, with the weight distributed between the claws and the two pads, which press into depressions in the surface. The head is strongly upturned, and the body is inclined outward between 10 and 20 degrees from the surface. From this position the bat can climb or jump into forward flight as described earlier. The turn after alighting is so rapid that the bat appears to alight upside down after a sharp banking turn toward the surface.

POSTCRANIAL OSTEOLOGY

Positional Terminology

FOLLOWING the practice of Vaughan (1959, 1966, 1970*b*, 1970*c*, 1970*d*), I have used the same positional terms for the bat body as employed for other vertebrates. The arm and manus (wing) are described as though fully extended in the middle of the downstroke (Fig. 24). The pollical side of the manus is anterior, digit V is directed posteriorly, digit IV is directed posterolaterally, and digits III and II are directed laterally to the level of the first interphalangeal joint of digit III. The terminal phalanges of digit III are oriented posterolaterad. The palmar surface of the hand and wing is considered ventral and the opposite side is considered dorsal. Following Norberg (1970*b*), the upper side of the bones of the arm is considered as dorsal, the lower side as ventral. Thus the ulnar side of the radius is posterior, the opposite side anterior. When strongly flexed, the forearm opposes the anterior surface of the humerus.

The hind limbs of a bat are oriented differently from those of other mammals, and positional terms for them are confusing. This problem is particularly severe in *Desmodus*, because the hind limbs are extremely mobile and can be oriented in more positions than those of other bats. For general descriptive purposes, the limb is considered as in flight during the first part of the downstroke (Fig. 19A) when it is oriented similarly to the hind limb of *Macrotus* (Vaughan, 1959). The plagiopatagial side of the limb is considered lateral, the opposite side is medial; thus the tibia is lateral, and the fibula is medial. The hind foot is oriented with the plantar side

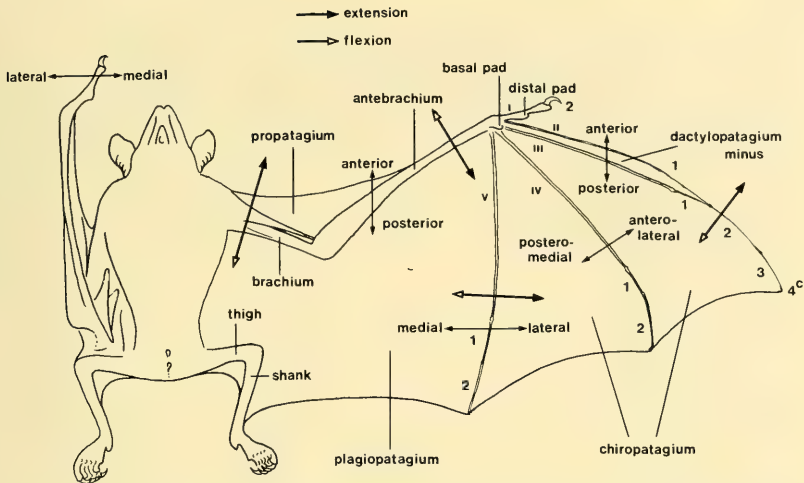


FIG. 24. Ventral view of *Desmodus* with parts of the flight membranes and positional terms relative to the arm, hand, and pelvic limb: I-V are metacarpals of corresponding digits and 1-4 are phalangeal elements; superscript "c" indicates the phalanx is cartilaginous. The right wing is folded as in terrestrial locomotion and the left wing is extended as in mid-downstroke of forward flight.

ventral and the opposite side dorsal. Movements in the plane of the wing membranes are termed either tibial or fibular. Digit V is located on the medial side of the foot and digit I on the lateral side.

Vertebral Column

Desmodus has seven cervical, 12 thoracic, six lumbar, five sacral, and no caudal vertebrae. Only the most significant features of the vertebrae are described below.

Cervical vertebrae.—The atlas and axis allow extreme lateral and vertical mobility of the skull, which is advantageous for making incisions in a host animal prior to feeding. The remainder of the cervical vertebrae are relatively short and broad and have well-developed transverse processes. These processes have a broad, flange-like projection ventrally and a thin posterodorsal projection that serves for the origin of the four slips of the *M. levator scapulae* on the last four vertebrae.

Thoracic vertebrae.—Anteriorly the vertebrae are relatively short

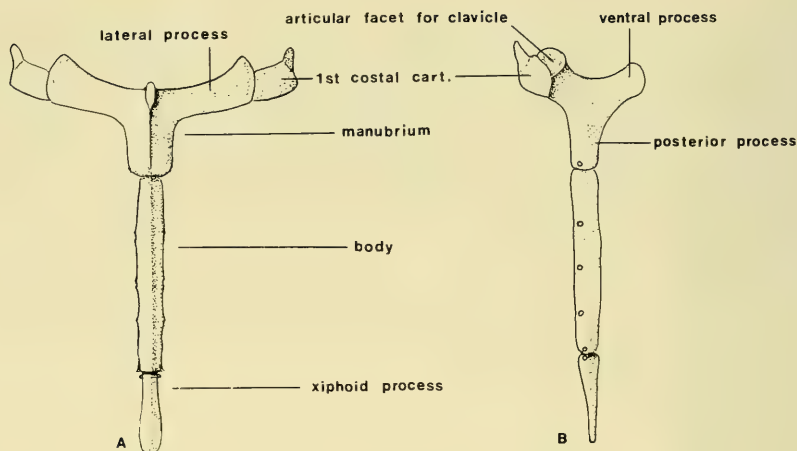


FIG. 25. Sternum and first costal cartilages of *Desmodus*. A, ventral aspect; B, lateral aspect.

and wide, and become increasingly longer and narrower posteriorly. The articulations between these vertebrae are similar to those of *Macrotus* as described by Vaughan (1959), but are more rigid, and the vertebral elements are closer together, providing a sturdy chain of bone.

A solid, tubercle-like, spinous process projects 1 mm dorsally from the mid-dorsal portion of the vertebral arch of the first thoracic vertebra. Bordered laterally by ridges that give rise to thin projections extending posteriorly beyond the border of the vertebra, it serves for the point of origin of the thickest portion of the trapezius muscles. The spinous processes of the next two vertebrae are represented by slight mid-dorsal elevations bounded laterally by prominent, posteriorly projecting ridges similar to those described on the first thoracic vertebra. On more posterior vertebrae, these ridges converge toward the midline and at the fifth thoracic vertebra, fuse medially to form a mid-dorsal ridge approximately 0.5 mm wide. On the sixth and successive vertebrae these ridges widen posteriorly to form a triangular dorsal prominence. The apex of the prominence on the last thoracic vertebra is directed anteriorly and is 1.2 mm in width at the posterior margin of the vertebra.

Lumbar vertebrae.—The mid-dorsal spinous processes are more

pronounced on the lumbar vertebrae. They become arrowhead-shaped, and the anterior point of one vertebra projects into a posterior indentation on the one before it. The spinous processes on the third, fourth, and fifth lumbar vertebrae are extremely high, and those of the fourth and fifth are low anteriorly and project strongly upward and backward. The centrum of the last lumbar vertebra is fused with the centrum of the first sacral vertebra and its transverse processes articulate laterally with the medial borders of the ilia.

Sacral vertebrae.—These are completely fused to each other and laterally to the medial aspect of the ilia. The fused vertebrae taper posteriorly into a laterally compressed rod of bone that arches posterodorsally for almost the length of the pelvic girdle. The posteroventral margins of the fused vertebrae are fused to the ischia immediately dorsal to the ischial tuberosities.

Sternum

In *Desmodus*, the sternum is composed of three distinct parts—manubrium, body, and xiphoid process—joined by thin cartilaginous discs. The manubrium has a laterally compressed and slightly anteriorly directed ventral process (Fig. 25A–B). Lateral processes project about 15 degrees dorsally and swing slightly anteriorly to enlarged distal ends, which have an anterolaterally and slightly dorsally oriented articular surface for the clavicle and a laterally directed articular surface for the first costal cartilage (Fig. 25A–B). A posterior process, approximately 2.5 mm long and triangular in cross-section, has a ventral apex that forms a thin ridge continuous anteriorly with the posterior edge of the ventral process. The articular facets of the costal cartilages of the second pair of ribs are located on the posterolateral surfaces of the posterior process.

The elongate body of the sternum is about 8 mm in length. It is roughly triangular in cross-section, slightly rounded dorsally, and, unlike many phyllostomatid bats, has no enlarged midventral keel. Articular facets for the costal cartilages of ribs three through six are arranged along the lateral borders at progressively shorter intervals (Fig. 25A–B).

The xiphoid process is slightly less than half the length of the body and is almost square in cross section in its anterior region.

The costal cartilages of the seventh pair of ribs articulate on the anterolateral aspects of the xiphoid process. Posteriorly the xiphoid process becomes dorsoventrally flattened and terminates in an expanded flange.

Ribs

The rib cage is about 1.4 times as broad and 1.1 times as deep as it is long. In one specimen, it was about 5 mm deep and 13.5 mm wide at its anterior end, and was expanded posteriorly to a depth of about 18 mm and breadth of 26 mm.

The first rib is strongly thickened anteroposteriorly as described by Vaughan (1959, 1970*b*) for other species of bats. A stout tubercle is found on the dorsal aspect immediately distal to the tuberculum. The rib arches gently dorsad and terminates in an expanded tip, which articulates with the thick, first costal cartilage. The costal cartilage is parallelogram-shaped and articulates on its dorsal surface with the first rib and on its medial surface with the lateral process on the manubrium. Inasmuch as the remaining costal cartilages of the sternal ribs are thin, the first costal cartilages provide much of the support of the sternum and reinforce it against the powerful dorsolateral pull of the sternal *M. pectoralis*. The second and third ribs are anteroposteriorly flattened, but caudally the ribs become dorsoventrally and laterally flattened. Rib seven is the last sternal rib, and the costal cartilage of rib eight connects with its costal cartilage. The cartilage of rib nine attaches to the costal cartilage of rib eight, but the cartilage of rib 10 connects directly with rib nine and the cartilage of rib 11 connects to rib 10. The twelfth rib is normally less than a millimeter long and has poorly defined distal connection.

Pectoral Girdle and Limb

Scapula (Fig. 26).—Viewed dorsally, the scapula is roughly elliptical posteriorly, truncate anteriorly, and about 41 per cent as wide as it is long. The glenoid fossa is directed slightly craniolaterally. The articular surface is anteroposteriorly elongated and is twice as high posteriorly as anteriorly. The posterior half of the fossa is deeply concave and strongly reinforced posteriorly by the expand-

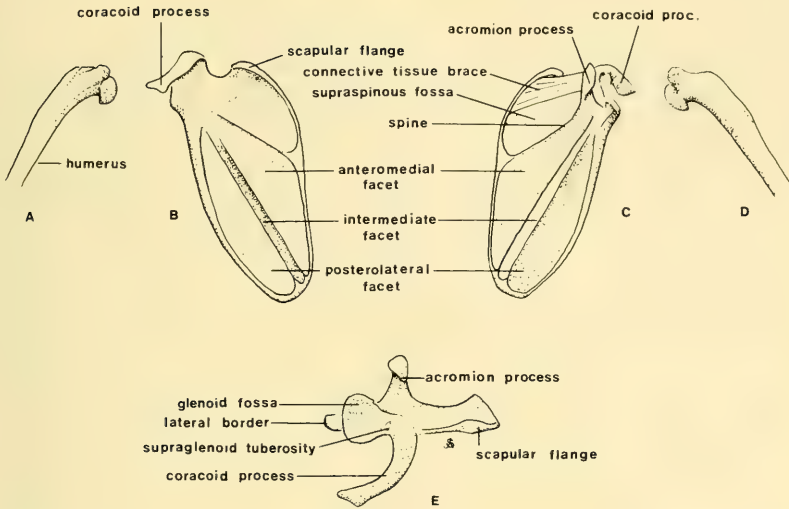


FIG. 26. Scapula and proximal portion of humerus of *Desmodus*: Ventral view of right humerus (A) and scapula (B); dorsal view of right humerus (D) and scapula (C); anterior view of right scapula (E).

ed lateral scapular border. Paired infraglenoid tuberosities are situated immediately posterior to the fossa and serve as points of origin for slips of the long head of the *M. triceps brachii*. The thick lateral scapular border slopes gently posteromedially and becomes progressively thinner toward the rounded posterior margin. The medial border, which is not as thick as the lateral border, is nearly parallel with the long axis of the body. Anteriorly, the medial border is thickened dorsoventrally and curves laterally to form the scapular flange. Lateral to the flange, the anterior scapular border is concave for about 2 mm, and then becomes thickened and directed anteriorly to form the projection that is the base of the coracoid process. Laterally, the thickened anterior process bears a small supraglenoid tuberosity that lies immediately anterior to the glenoid fossa.

The anteroposteriorly flattened coracoid process extends ventrally from the thickened anterior projection of the scapula, medial to the supraglenoid tuberosity, and then curves laterally and slightly posteriorly. The tip of the coracoid process is expanded and lies below and slightly lateral to the middle of the glenoid fossa.

The dorsal surface of the scapula is transected by the scapular

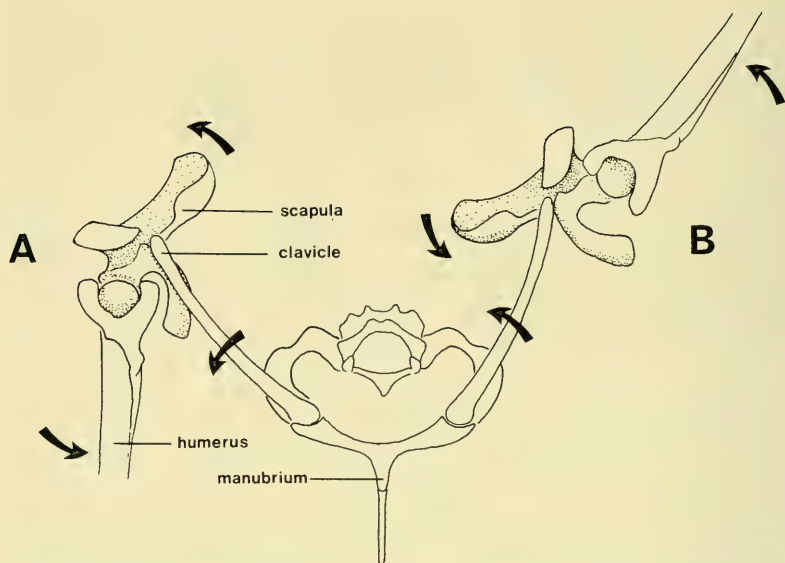


FIG. 27. Diagrammatic frontal view of the pectoral girdle of *Desmodus*: A, right clavicle and scapula tipped ventrally and right humerus fully adducted as might occur at the end of a jump; B, position of left clavicle, scapula and humerus at the start of a jump or downstroke. The lateral scapular border is tipped upward and the humerus is locked dorsally with the scapular border.

spine, which runs from the medial border anterolaterally toward the posterior half of the glenoid fossa. Quite low medially, the spine becomes progressively higher laterally and, about 4 mm from the glenoid fossa, curves sharply cranially and dorsally to the anteroposteriorly flattened acromion process. The distal 3 mm of the acromion process is thickened and strongly anteroventrally curved so that it lies medial to, and above, the glenoid fossa. The lateral border of the acromion process arises about a millimeter medial to the highest point of the glenoid fossa. A strong band of connective tissue runs from the dorsolateral aspect of the flange to the medial surface of the expanded tip of the acromion process, and helps brace the latter against the pull of the abductors and supinators of the humerus. The anteroposterior flattening of the process and the increased height of the scapular spine also aid in resisting these forces.

In *Desmodus*, the supraspinous fossa is smaller relative to the

infraspinous fossa than in some of the closely related phyllostom-
atids. A thickened ridge extending from the base of the acromion
process to the anteromedial edge of the posterior border separates
the large anteromedial facet from the small and nearly vertically
oriented intermediate facet. Another thickening separates the in-
termediate facet from the nearly horizontally-oriented postero-
lateral facet. The vertical orientation of the intermediate facet pro-
vides a solid surface for muscular attachment and reduces the
relative width of the entire facet. This suggests that the muscle
mass that originates there, the *M. infraspinitus*, is suited for pow-
erful contraction in a limited direction. Posteriorly the scapula ter-
minates in a cartilaginous extension typical of many other bats.

Clavicle (Fig. 27).—The proximal articular surface is greatly en-
larged, rather ovoid, and elongate laterally. Within 2 mm of the
articular surface, its diameter constricts to about a millimeter. At
this point the clavicle is nearly circular in cross-section, but becomes
laterally compressed distally.

In specimens preserved with the wing folded in the typical pos-
ture seen in hanging, the long axes of the proximal half of the
clavicles are oriented about 20 degrees anterolateral and about 30
degrees anterodorsal to the long axis of the body. From their prox-
imal articulations, the clavicles curve gently posterodorsally and,
over the proximal 80 per cent of their length, become increasingly
deeper (anteroposteriorly) in cross-section. The distal 20 per cent
of each clavicle is curved sharply posteriorly, and the slightly ex-
panded distal tip is displaced about 3 mm posterior to the long
axis of the proximal shaft.

The ventrolateral aspect of the distal 1.5 mm of the clavicle is
bound by tough connective tissue to the ventromedial surface of
the anterior tip of the scapula. The articular surface is elongate
and nearly horizontal, a configuration that permits the scapula to
tilt about its long axis relative to the clavicle. Angular displacement
of the long axis of the scapula is limited to only a few degrees by
the articulation. However, when the lateral scapular border is
rocked strongly ventrally, the articulation allows the long axis of
the scapula to be inclined upward posteriorly between 10 and 15
degrees. This suggests that the anterior end of the scapula is com-
monly tipped ventrally when the lateral scapular border is tipped
ventrally, as in a jumping maneuver or in certain terrestrial feeding
postures. This helps explain the apparent depression of the shoul-

der joint during these movements. The curvature of the posterior surface of the clavicle, adjacent to its distal tip, perfectly matches the curvature of the coracoid process, and allows the coracoid process to swing behind the clavicle (Fig. 27A). The scapula can be rotated about its long axis to position the coracoid process directly behind the clavicle. When the clavicle is inclined a normal 40 degrees above horizontal (viewed frontally), this rotation of the scapula orients the short scapular axis vertically, thus directing the glenoid fossa ventrally. This is the most striking feature of the pectoral girdle osteology of *Desmodus* and is partly responsible for the high quadrupedal stance and remarkable jumping ability of the species, as it allows the humerus to be directed completely ventrally.

At the clavo-scapular articulation, the surfaces of both the clavicle and scapula are bordered dorsally by nearly vertical bony surfaces that limit upward rotation of the lateral scapular border. When the short axis of the scapula is within a few degrees of being parallel to the long frontal axis of the clavicle, following upward rotation of the lateral scapular border (Fig. 27B), the supra-articular surfaces meet and stop further rotation. Rotational forces applied to the scapula are thus transferred to the clavicle. A strong connective tissue band runs from the middle anterior surface of the clavicle to the middle of the coracoid process and aids in stopping the upward lateral rotation of the scapula. The articulation of clavicle and scapula allows rotation of the short axis of the scapula through an arc of fully 120 degrees.

Humerus (Figs. 26–28).—This bone is relatively stocky in *Desmodus*; the greatest diameter of the middle diaphysis is about 5.4 per cent of the length. The head is directed posterior to the proximal end of the shaft. Anterior to the head is a deep depression (Fig. 28E) into which the supraglenoid tuberosity fits when the humerus is extended anteriorly. The greater tuberosity extends posterodorsally and medially from the medial end of the shaft. The ridge of bone that runs between the tuberosity and the dorsal aspect of the head articulates with the dorsal border of the glenoid fossa to stop abduction of the humerus (Fig. 27B). Anteriorly, the greater tuberosity gives way to a ridge that projects anteroventrally to meet the medial end of the pectoral ridge. The lesser tuberosity projects posteroventrally and medially from the medial end of the shaft, and is continuous laterally with a low midventral ridge that extends

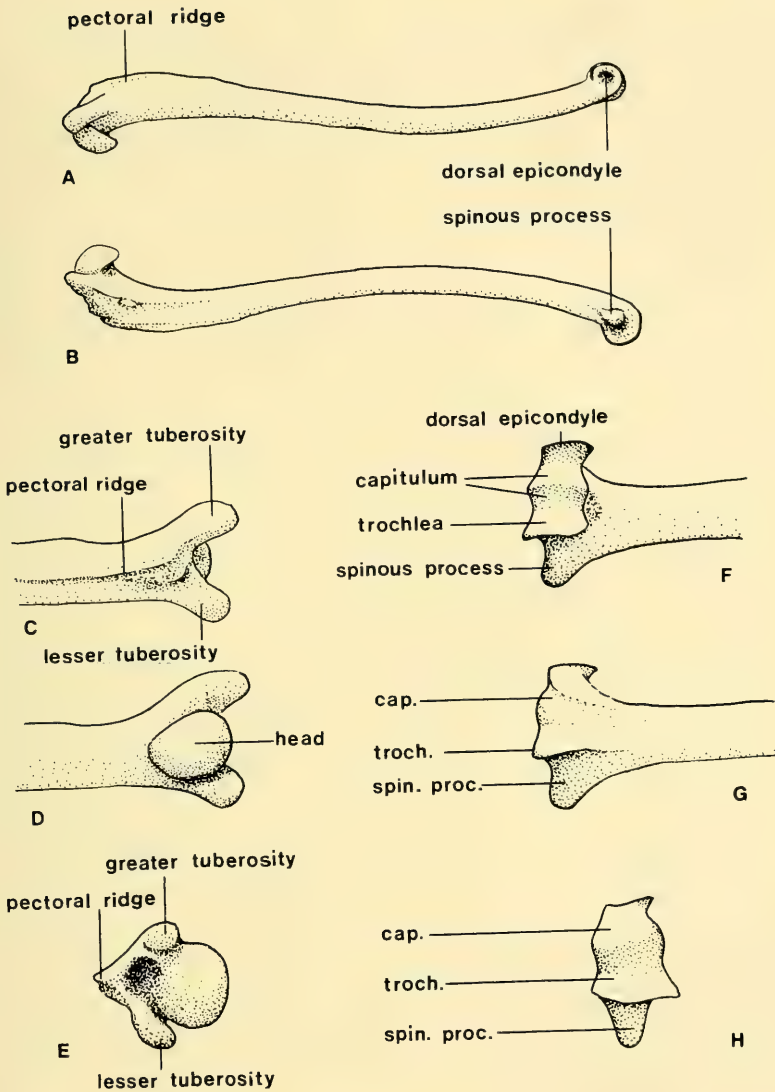


FIG. 28. Humerus of *Desmodus*: A, dorsal view; B, ventral view; C, anterior view of proximal end; D, posterior view of proximal end; E, medial view of proximal end; F, anterior view of distal end; G, posterior view of distal end; H, lateral view of distal end.

for several millimeters along the shaft and ends in a small tubercle about 6.5 mm distal to the tip. A ridge runs anterodorsally from the lesser tuberosity to the ventromedial base of the pectoral ridge. The importance of the rotative forces applied by the muscles that insert on the greater and lesser tuberosities is reflected by the ridges that run from their bases anteriorly to the medial end of the pectoral ridge.

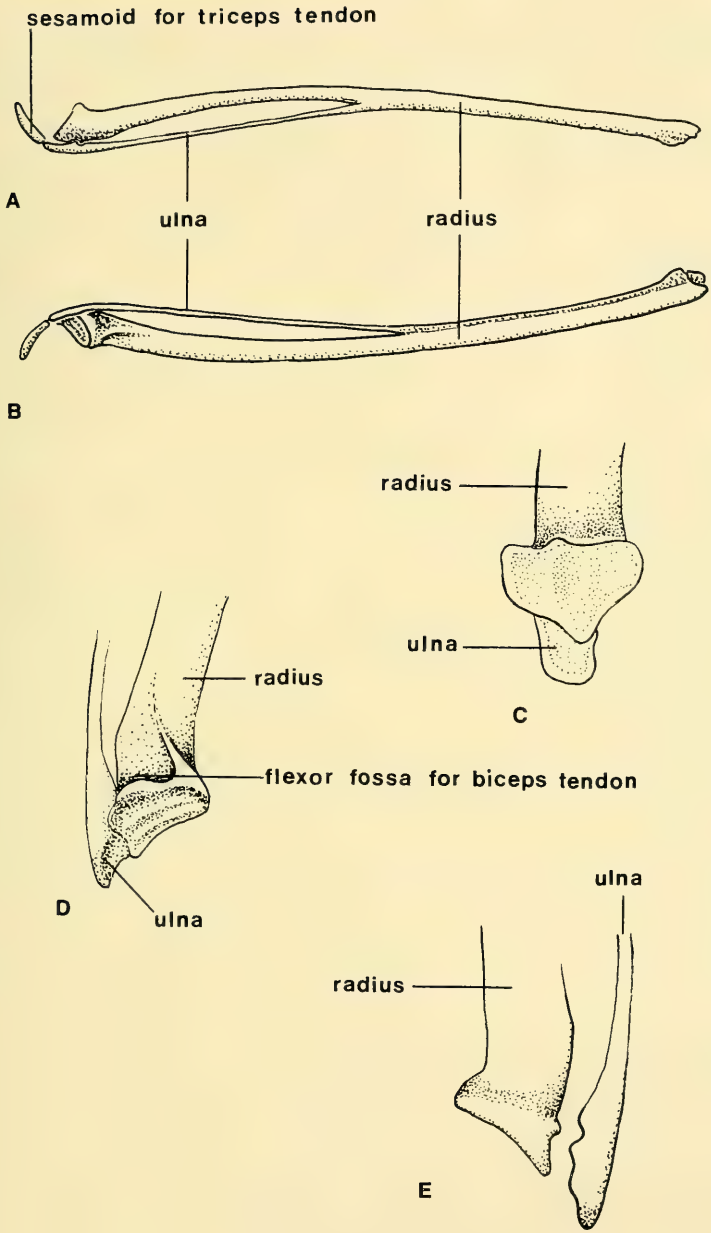
The pectoral ridge projects anteriorly about a millimeter from the middle of the proximal end of the shaft, beginning adjacent to the head, and continues distally for about 8 or 9 mm. The ridge is divided in its middle part into two ridges, one below the other, but it becomes quite thin about 2.5 mm distal to that point and is thin for the remainder of its length.

For the first one-fourth of its length, the shaft is quite straight and roughly circular in cross section except for the pectoral ridge. The distal three-fourths of the shaft is strongly bowed posteriorly and compressed anteroposteriorly. The anterior aspect of the distal half is slightly concave. These structural features apparently strengthen the distal shaft against the torque and strong upward forces encountered in the wingbeat cycle and terrestrial locomotion. The bowing of the distal three-fourths accomodates the prominent forearm musculature when the forearm is strongly flexed toward the humerus during terrestrial locomotion.

The locking mechanism between the humerus and scapula of other bats described by Vaughan (1959) and others is quite evident in *Desmodus* and limits adduction and abduction to about 30 degrees above and below the short axis of the scapula (Fig. 27). However, the depression anterior to the head of the humerus is sufficiently deep, and the supraglenoid tuberosity is sufficiently small and anteriorly positioned, that the humerus can be extended to within 30 degrees of the long axis of the lateral scapular border before being stopped by this locking mechanism. Anterior extension of the humerus is necessary for alighting on a horizontal surface (Fig. 23), a backward jump (Fig. 12), and climbing on a vertical surface (Fig. 6).

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FIG. 29. Right radius and ulna of *Desmodus*. A, dorsal view; B, ventral view; C, anteromedial view of proximal end; D, ventral view of proximal end; E, dorsal view of proximal end.



The distal articular surfaces formed by the capitulum and the trochlea are displaced anteriorly and slightly dorsally to the axis of the shaft (Fig. 28F–H). The groove separating the two inclined surfaces of the capitulum is rather shallowly concave, whereas the groove separating the capitulum from the ventral trochlea is deeper and rather V-shaped in section. The prominent ventral flange of the trochlea continues to the posterior side of the epiphysis, where the groove above it is broadened and bordered above by the ridgelike, posterior continuation of the dorsal side of the capitulum. The ulna and the elongate sesamoid of the *M. triceps brachii* tendon (Fig. 29A–B) run into this groove as the forearm is extended. The epicondyle above the capitulum is indented (Fig. 28A), and the *M. supinator* arises from the center of this indentation. Proximally, a small ridge runs posteromedially to the shaft and serves for the point of origin of the *M. extensor carpi radialis longus* and *M. extensor carpi radialis brevis*. Ventrally, the epicondyle (medial epicondyle) extends slightly more than 2 mm to form a spinous process (Fig. 28B, 28F–G). The tip of this process is located directly below the center of rotation of the radius; thus, flexion and extension of the radius do not affect the length of the muscles that originate on the spinous process.

Radius and ulna (Fig. 29).—The radius is about 1.6 times the length of the humerus and over its proximal half curves strongly posteriorly and ventrally (Fig. 29A–B). The proximal articular surface is directed anteromedially and has a central concavity that is bordered dorsally and ventrally by low ridges and adjacent flattened areas (Fig. 29B–D). The rounded ventral part of the capitulum fits into the central concavity, and the inclined dorsal portion of the capitulum and the ventral trochlea articulate with the narrow flattened surfaces above and below the concavity. The concavity is in line with the axis of the shaft and is bordered ventrally by a flange that makes up the ventral articular surface. A prominent ridge of bone extends from the anterior border of this surface, at the level of the bottom of the concavity, laterally for about 5 mm (Fig. 29B, 29D). Posterior to this ridge is a flattened, posterodorsally inclined surface that ends in a deep groove (the flexor fossa) on the posterior face of the radius. The tendons of the *M. biceps brachii* and *M. brachialis* run ventrally over the ridge immediately distal to the ventral flange and insert into the flexor fossa. Thus, contraction of these muscles exerts both a flexive force to

the forearm and a powerful supinating force to the entire arm, as the articulation of the humerus and radius severely limits any movement except flexion and extension.

The thickened proximal end of the ulna is positioned posterior to the ventral half of the proximal articular surface of the radius and projects 1.5 mm beyond its proximal tip (Fig. 29A, 29D). A vertical groove on the anterior surface of the ulna articulates with a ridge on the posterior surface of the radius about 1.5 mm distal to its end. A groove distal to the ridge on the radius accepts a ridge on the ulna. This tongue-in-groove mechanism stabilizes the ulna against the medial pull of the *M. triceps brachii*. Distal to the thickened proximal articular area, the shaft of the ulna is thin and concave anteriorly. The ulna is fused distally to the posterodorsal surface of the radius at about the middle of the radial shaft. The rigid fusion distally and strong articulation proximally suggest that the ulna is important in bracing the radius against forces directed toward its long axis during terrestrial locomotion or jumping. It also affords a rigid structure for muscle attachment. Distal to the fusion of the ulna and radius, a thin ridge runs along the posterodorsal surface of the radius to within 5 mm of its distal end. The ridge is the same thickness and width as the ulna before its fusion to the radius. Although no embryologic evidence is available, this ridge may represent the distal end of the fused ulna. The concave underside of this ridge serves for muscle attachment. Distal to the fusion of the ulna with the radius, the radius is diamond-shaped in cross section. The broad, anterodorsal surface of the distal 2 or 3 mm is divided by bony ridges into grooves for the tendons of several of the forearm muscles (Figs. 30–31). Anteroventrally, two ridges of bone make a deep channel for the *M. abductor pollicis longus*. The large, posterodorsal ridge bordering this channel is the anteroventral edge of a pair of channels divided by a small median ridge. The lower channel accommodates the *M. extensor carpi radialis longus* and the upper accommodates the *M. extensor carpi radialis brevis*. Posterodorsally, a broad flat surface separates these channels to form a prominent posteriorly-projecting flange at the distal tip of the radius. This flange is the dorsal edge of a channel bordered ventrally by a median projection of the cuneiform. The tendons of the *M. extensor pollicis brevis*, *M. extensor digitorum communis* to digits III and IV, and the *M. extensor indicis* run through this channel. On the posterior surface of the radius medial to this

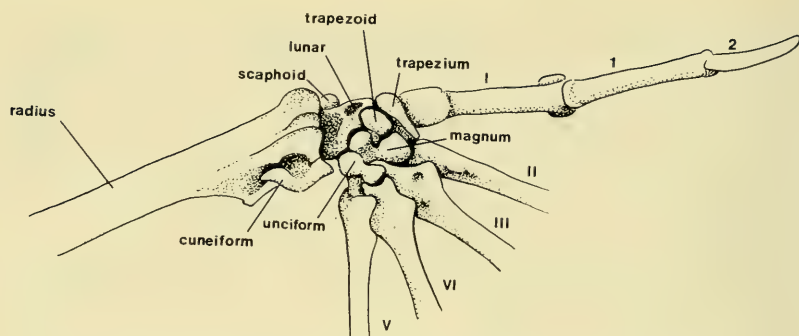


FIG. 30. Dorsal view of the right carpus and first digit of *Desmodus*.

channel is a large backward-projecting flange of bone that supports the tendons ventrally and functions as a posterior extension of the ventral aspect of the channel described above. This flange on the radius also forms a shelf for the tendon of the *M. extensor digiti quinti proprius* to digit V and the tendon of the *M. extensor carpi ulnaris*. The tendons are bound to this shelf of bone by a tough ligamentous band, which runs from the posterior tip of the shelf to the posterior tip of the cuneiform. The exceptional investment of the distal portion of the radius with grooves and ridges of bone to confine tendons reflects the great forces placed upon the tendons, and thus elements in the hand, during terrestrial locomotion, jumping, and initial flight.

The distal articular surface of the radius is deeply concave and directed posterolaterally from the long axis of the shaft. The posteroventral surface of the border of the articular surface bears a prominent lateral projection, which interlocks with the deep notch in the posterior aspect of the lunar. The edge of the articular surface posterodorsal to the projection forms a ridge that serves to hold the lunar in position. Anteroventrally, the projection continues as a ridge of bone that confines the lunar ventrally and helps limit it to movement on only one plane.

Manus (Figs. 30–31).—The lunar is the largest of the eight carpals and is elongate parallel to the long axis of the distal articular surface of the radius. The body of the lunar is offset posteroventrally to the long axis of the shaft and bound to the shaft by heavy ligaments on the posterodorsal surface. On the posteromedial aspect of the lunar is a deep groove that interlocks medially with the

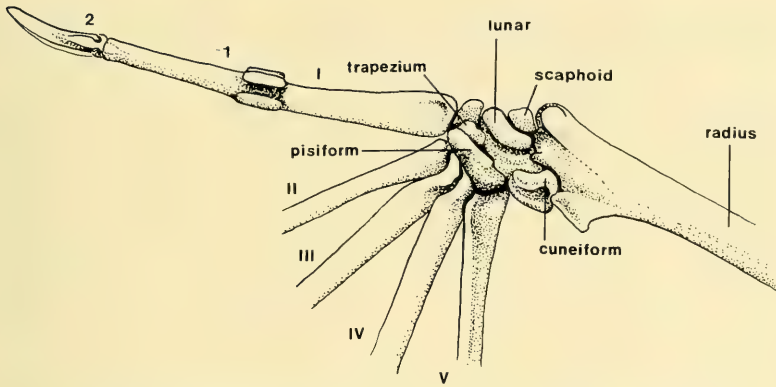


FIG. 31. Ventral view of the right carpus and first digit of *Desmodus*.

distal projection on the posteroventral side of the articular surface of the radius and limits flexion of the lunar. The cuneiform is tightly bound to the radius posterodorsally to the lunar and bears a posteromedial projection that forms the ventral half of the deep channel described above. The posterior tip of this projection curves strongly dorsally, making the channel almost tubular (Fig. 30).

A cylindrical anteroventral projection of the lunar bears a smooth surface anteriorly on which the small ovoid scaphoid rests. A deep circular groove separates the projection posterodorsally from an expanded circular ridge perpendicular to the long axis of the lunar. This groove accommodates a prominent anteromedial projection from the flattened trapezium and stabilizes it as the carpus is flexed and extended. The anterodorsal surface of the lunar posterior to the lateral ridge is saddle-shaped and accommodates an anteromedial projection of the small trapezoid that projects from beneath the overlying trapezium. The lateral articular surfaces of the lunar limit the movements of the trapezium, trapezoid, magnum, and cuneiform to a single plane, that of lateral extension and medial flexion.

Distally, the cuneiform projects anteroventrally parallel to the long axis of the lunar and forms a broad articular surface that contacts the posteromedial aspect of the cuneiform. The trapezoid, which rides against the posterodorsal surface of the ridge on the lunar, serves as a spacer between the trapezium and the adjacent

magnum. The magnum bears a prominent posteroventrally-directed spine beneath the rounded articular surface, which slides against the deep lateral depression of the lunar. As the magnum is flexed, this spine locks against the posterior surface of the lunar. Distal to its articulation with the lunar and the cuneiform, the unciform is expanded and bears on its posterior surface a deep groove bordered above and below by slightly convex articular surfaces. The long axis of the groove is inclined medially, slightly above the long axis of the radius, and accommodates the fingerlike projection on the proximal end of metacarpal IV. The surfaces above and below the groove accommodate proximal portions of metacarpals IV and V, respectively. Distally, the arrangement of the trapezium, trapezoid, magnum, and cuneiform produces deep notches on the posterolateral surface of the carpus, which receive the proximal processes of metacarpals II and III.

The long axis of the rodlike pisiform is oriented obliquely across the posterior surface of the carpus from the medial projection of the trapezium adjacent to its articulation with the lunar posterodorsally to the posteromedial tip of the cuneiform. Heavy ligaments bind the pisiform to the posteromedial tip of the cuneiform, the posteromedial surface of the magnum, and the medial tip of the trapezium. A large tubercle projects from the posterior surface of the pisiform immediately ventrad to its dorsal tip, which is flattened into a smooth articular surface. This dorsal articular surface meets the flattened and slightly ovoid ventral surface of the proximal tip of metacarpal V. The articular facet on the metacarpal is oriented ventral and perpendicular to the slightly concave proximal articular facet that contacts the cuneiform.

Digit I (Figs. 30–31).—The proximal articular surface of the first metacarpal slopes anterolaterally from its ventral ligamentous attachment to the broad, flattened, distal surface of the trapezium, which slopes anteromedially. The articulation allows considerable freedom of movement, and the first metacarpal can be adducted or abducted through an angle of about 130 degrees. The first metacarpal is the thickest of the metacarpals and about 7 mm long, longer than the entire pollux of most other microchiropteran bats. Its thickness reflects the forces it bears in terrestrial locomotion and jumping. The distal articular surface is rounded, allowing movement of the first phalanx in almost any plane. The proximal articular surface of the first phalanx is deeply concave to accom-

moderate the rounded articular surface of the metacarpal, and the hingelike distal articular surface limits movement of the short second phalanx (which bears a recurved claw), to flexion and extension.

Digit II (Figs. 30–31).—The proximal end of the second metacarpal is vertically expanded and compressed anteroposteriorly into a rounded flange, which articulates in the groove between the trapezium and the magnum. The anterior tip of the flange rests against the posterolateral tip of the trapezoid. Distally, there is a ventral tubercle that articulates with the proximal part of metacarpal III. Two millimeters distal to this tubercle there is a small posterodorsal saddle, bordered distally by a tubercle, into which articulates the large, anterodorsal tubercle of metacarpal III. This is the spacer described by Vaughan and Bateman (1970) that maintains the spread of the second and third metacarpals in bats with a large dactylopatagium minus. Because *Desmodus* does not have a large dactylopatagium minus, this tubercle is quite small.

The second metacarpal is approximately 81 per cent of the length of metacarpals III through V. Its distal articular surface and the proximal articular surface of the first phalanx are expanded, flattened, and nearly perpendicular to the long axis of the digit. Firm ligamentous binding of the joint limits movement and stabilizes the leading edge of the chiropatagium. The second phalanx is cartilaginous and serves only as a connection between the second and third digits to stabilize the leading edge of the chiropatagium.

Digit III (Figs. 30–31).—Medially the metacarpal is enlarged and flattened into a vertically-oriented flange similar to, but larger than, the flange of metacarpal II. The flange fits into a shallow curved depression on the posterior surface of the magnum and is bordered posteriorly by the concave, flattened anterolateral portion of the distal part of the cuneiform. There is a prominent depression on its posterior surface that accommodates an anteriorly-directed process on the anteroventral aspect of the proximal tip of metacarpal IV. The distal articular surface of metacarpal III is expanded to one and a half times the diameter of the distal shaft and, along with the proximal articular surface of the basal phalanx, is perpendicular to the long axis of the shaft. The long axis of the shaft of the basal phalanx is offset dorsally and in line with the dorsal aspect of the shaft of the metacarpal. The metacarpophala-

langeal joint allows limited movement in any direction, but ligamentous binding limits upward deflection. Much of the stability of this joint is provided by medially directed forces imparted by the tendons inserting on the first phalanx. Compression of the shaft forms a ventral notch proximal to the distal articular surface. The trochlealike articular surface bears a shallow vertical groove on its dorsal and distal surface. The proximal articular surface of the second phalanx is deeply concave and bears a dorsomedian process that curves strongly proximad to articulate dorsally with the groove of the distal surface of phalanx one. Lateral processes of phalanx two articulate medially with the lateral edges of the trochlea of the first phalanx and limit the movement of this joint to a vertical plane. The second phalanx can be deflected about 30 degrees above the long axis of the metacarpal and first phalanx, but this movement is then stopped by the dorsomedian process of the second phalanx. Ventral flexion through an arc of more than 90 degrees is possible as the ventral aspect of the articular surface of phalanx two fits into the notch proximal to the distal tip of the first phalanx. The second interphalangeal joint is flattened and similar to the metacarpophalangeal joint. All but ventromedial flexion is restricted by a firm ligamentous binding.

Digits IV and V (Figs. 30–31).—From the anterolateral aspect of the proximal articular surface of metacarpal IV, a spine projects anteriad to fit into the depression on metacarpal III. This serves as a center of rotation that allows upward deflection of the fourth metacarpal. However, if the hand is extended, a flange on the anterodorsal edge of metacarpal IV slides into the posteriorly-turned dorsal edge of the articular flange of metacarpal III and stops this movement. This effectively braces the fourth metacarpal against upward displacement from the forces of the airstream as the extended wing is adducted. A posteromedially directed fingerlike projection of the proximal articular surface of metacarpal IV articulates with the groove in the distal surface of the cuneiform. The depression dorsal to the projection fits over the convex surface above the groove on the cuneiform. This arrangement prevents any rotation of the shaft, which would reduce the effectiveness of the dorsal bracing previously described.

The proximal surface of metacarpal V bears a central notch that fits against the fingerlike posteromedial projection of the fourth metacarpal. Dorsally, a projection of the fifth metacarpal fits into

a depression on the posteromedial and dorsal aspect of the fourth metacarpal and prevents upward deflection of the fifth metacarpal when the wing is extended and forced downward against the air-stream.

The ventromedial surface bears a tubercle that projects antero-laterally and fits into a groove on the posteromedial and ventral part of metacarpal IV. Strong tendinous binding here further braces the fifth metacarpal against upward deflection by the air stream. Medial to the central notch, a flat articular surface curves posteriorly and articulates with the flattened distal surface of the cuneiform below the groove that accommodates the fingerlike projection on metacarpal IV. The distal articular surfaces of the fourth and fifth metacarpals are similar to that of the third, but typically slope proximally on their ventral edge, allowing ventral flexion of the first phalanges through an arc of more than 90 degrees as the wing is folded. The proximal articular surfaces of the first phalanges of digits III and IV are flattened and similar to that of the first phalanx of digit III.

The first interphalangeal articulations of digits IV and V are similar to the first interphalangeal articulation of digit III. Digits IV and V have similar dorsomedial projections on the proximal articular surfaces of the second phalanges, which, unlike the less restrictive arrangement seen at the first interphalangeal joint of digit III, limit upward deflection of the second phalanges to a position parallel to the long axis of the basal phalanges. As the metacarpophalangeal joints allow considerable upward deflection, there is little need for additional deflection at the interphalangeal joints. However, ventral flexion through an arc of more than 100 degrees is permitted to facilitate folding of the wing. Lateral movements of the distal phalanges of digits IV and V are limited by ligamentous binding, which holds the second phalanges by their lateral articular surfaces against the distal articular surface of the basal phalanges, and by proximolateral projections, which articulate with the distolateral surfaces of the basal phalanges.

FUNCTIONAL MYOLOGY OF THE PECTORAL GIRDLE AND LIMB

IN the following descriptions I follow the system of muscle terminology used by Vaughan (1959) who, in turn, followed those of Hill (1937) and Rinker (1954). However, I have used the same positional terms as in the previous section on osteology. Thus, the body, arm, and hand are described as in forward flight with the wing fully extended in mid downstroke.

Comments on Electromyographic Analysis

Without implant of a tension transducer in series with the insertional tendon of a specific muscle, there is no way of determining the exact amount of tension that a muscle exerts on its insertion and origin or the temporal distribution of that tension in normal movements.

However, electromyography provides useful information about both parameters if the electromyographic record is accurately interpreted. Bigland and Lippold (1954) and Bergstrom (1959) have demonstrated that tension varies directly with the integrated potential changes and that spikes of an electromyogram can be used to estimate the relative tension generated by a given muscle. Bas-majian (1962) suggested that the number of spikes, the degree of their superimposition, and their relative height and type, are important factors in analysis of muscular function through an electromyogram. He stated: "Experience has shown that the easiest, and in most cases, most reliable evaluation is by the trained observer's visual evaluation of results colored by his knowledge of the technique involved." I have made no attempt to precisely quantify the data, but have discussed it in such relative terms as "no contraction," "slight contraction," or "strong contraction." Until electromyographic data are available for all the major muscles of a particular part of the girdle or limb, or the exact force produced can be determined from implanted tension transducers, any attempt at a more precise quantification easily could be misleading.

Electromyographic data, however, do allow more accurate analysis of the function of many muscles than heretofore has been

possible. All of the literature on the function of muscles in bats is centered around predictions about the role of a given muscle based on strictly positional criteria. Although reasonably reliable conclusions can be drawn from positional relationships, they can be nicely supplemented and clarified by electromyographic data.

The temporal lag between myopotential changes and force generated by a muscle, which is a function of the time between depolarization and shortening of the fibers and the time required to stretch the elastic components of the muscle, probably varies between muscles in *Desmodus*. For the coracoid head of the *M. biceps brachii*, this delay was experimentally determined to be approximately 10 milliseconds. A tension transducer was attached to the insertional tendon of this muscle and the electromyogram from the muscle and output from the transducer were recorded simultaneously with the high-speed camera. Restraints of time and availability of additional living specimens for these experiments prevented doing this with other muscles. When such data are available, the electromyographs might be interpreted differently. However, as presently interpreted, they provide considerable insight about the function of muscles in the pectoral girdle and limb.

The points on the electromyographic traces in Figs. 32–33, and 35–41 coincide temporally with corresponding drawings of the locomotor behavior. Both the electromyogram and drawings are labeled with upper case letters. The probable time of muscular contraction, represented by a solid line, is displaced to the right along the horizontal axis of the electromyogram, a distance corresponding to 10 milliseconds. A scale indicating the magnitude of the potential changes on the vertical axis and time on the horizontal axis is included in each figure.

Muscles Unique to Bats

M. occipito-pollicalis (Figs. 42, 44).—The anatomical modification of this muscle in *Desmodus* seems quite different from that in other bats (Macalister, 1872; Humphry, 1869; Vaughan, 1959; Norberg, 1970*b*). There is considerable variability between species in the relative length of the fleshy belly distal to its origin on the cranium, and in some bats, such as *Plecotus auritus* (Norberg, 1970*b*) and *Pteropus edwardsi* (Humphry, 1869), there is a second, distal belly.

However, descriptions of this distal belly indicate it is relatively fusiform and originates almost entirely on the rather compact insertional tendon of the proximal belly, which runs along the leading edge of the propatagium (Fig. 24). In *Desmodus*, the proximal belly inserts rather diffusely into the proximal propatagium. A broad, flat belly originates from fibers in the anterior half of the propatagium anterior to the radius, about one-third the distance toward its distal tip, and from some of the small insertional tendons of the proximal belly. Schumacher (1932) described a *M. propatagialis proprius* in *Pteropus* that was innervated by nerves of the cranial portion of the brachial plexus, whereas Macalister (1872) found the proximal belly in three other genera to be innervated by the spinal accessory nerve. I was unable to trace the innervation of either muscle, but on strictly positional criteria, I designate the proximal belly as *M. occipito-pollicalis* and the distal belly as *M. propatagialis proprius*.

Origin is primarily on connective tissue lateral to the midline from the posterior tip of the sagittal crest and down the supraoccipital for 2 mm. A distal slip originates from fibers of the clavicular *M. pectoralis*. Insertion is by a finely branched tendon onto the connective tissue fibers of the propatagium at the level of the base of the forearm.

In contrast to the condition in most other bats, the *M. occipito-pollicalis* tenses the propatagium directly by drawing its elastic fibers anteromediad. As in other bats, it depresses and tightens the leading edge of the propatagium. Contraction of the fibers of the clavicular *M. pectoralis*, which insert on this muscle, draws the medial half of the propatagium strongly ventrad and increases the camber of the medial portion of the wing.

M. propatagialis proprius (Fig. 46).—The origin is from the fibers in the anterior half of the middle propatagium and on some of the insertional fibers of the *M. occipito-pollicalis*. Insertion is by an aponeurosis over the medial aspect of metacarpal I, a thin tendon to an aponeurosis over the metacarpophalangeal joint of digit I, and a tendon on the middle of the anterior surface of the first phalanx of digit II.

This muscle is not effective in moving the digits, but uses them as a fulcrum to tense the propatagium. The vertical orientation of the wing during the first half of the upstroke and its position anterior to the body may have necessitated the development of this

muscle. When the wing is highly flexed in this phase of the upstroke, contraction of the *M. occipito-pollicalis* would have only limited effect if it inserted on the hand. However, tension from both proximal and distal sides of the propatagium, directed against the fibers posterior to the leading edge, is effective in reinforcing it for a firm airfoil. Contraction of both muscles at the start of the coasting phase of the jump would keep the propatagium oriented ahead of the arm and somewhat reduce its area and drag. This muscle also serves to help brace the leading edge of the medial wing as it is deeply pronated for thrust production in the downstrokes during accelerating flight.

M. coraco-cutaneus (Fig. 44).—Origin is on the medial aspect of the tip of the coracoid process of the scapula. The belly gives rise to a second belly about 5 mm distal to the origin on the coracoid process, and both bellies insert onto elastic fibers in the plagiopatagium posterior to the brachium and proximal one-fourth of the forearm.

When the wing is adducted in the downstroke, contraction helps reinforce the plagiopatagium and reduce billowing from the force of the air stream. In the first half of the upstroke, when the distal half of the wing is oriented vertically and raised anterior to the body (Fig. 20), contraction of this muscle and pull from the hind limbs probably help maintain tension on the plagiopatagium to reduce its surface area and minimize drag.

Muscles of the Pectoral Girdle and Limb

Trapezius Group

M. clavotrapezius (Fig. 42).—This muscle has its origin on a tough tendinous sheet bound to the anterior tip of the dorsal process on the first thoracic vertebra and to a dorsal tubercle on the first rib. It inserts over the dorsal surface of the clavicle, beginning about 9 mm distal to its proximal tip and continuing to within 2 or 3 mm of its distal tip.

In contrast to the condition in many other species of bats, the clavotrapezius is separate from the acromiotrapezius. It is much larger than the anterior portion of the united clavotrapezius and acromiotrapezius, which insert on the clavicle of other species. Contraction pulls the distal end of the clavicle, and thus the anterior end of the scapula, dorsomedially. The relatively free artic-

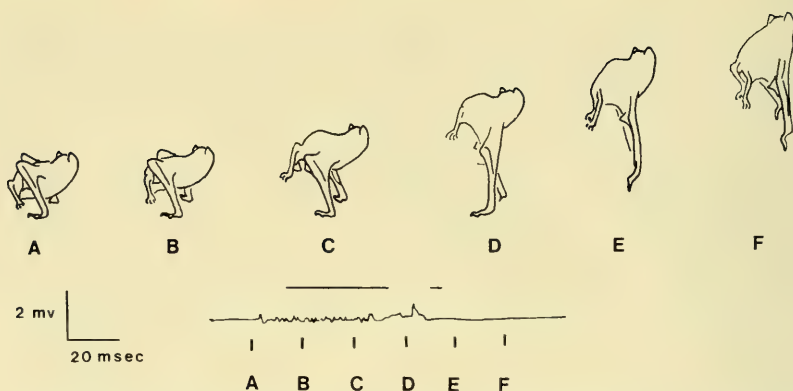


FIG. 32. Electromyogram of right *M. clavotrapezius* of *Desmodus* and corresponding locomotor behavior. The contraction of the muscle occurs slightly after the electrical event and is shown as a solid line above the electromyographic recording. Corresponding locomotor stages and portions of the electromyogram are indicated by the same letters.

ulation of the scapula and clavicle of *Desmodus* requires that the clavicle be firmly braced to provide a solid fulcrum on which the scapula can rock about its long axis, as described in other species of bats by Vaughan (1959). However, more importantly, the anterior tip of the scapula, and thus the shoulder joint, can be pulled dorsomedial by this muscle. This movement is important in *Desmodus* to position the wing prior to the first downstroke after a jump. The shoulder is pulled ventrad during the jump and must be positioned dorsally to give the ventral flight musculature a good mechanical advantage on the downstroke. Electromyographic data illustrate that the contraction of this muscle probably occurs during the powered phase of the jump to stabilize the clavicle. Assuming a 10 millisecond temporal lag between the myopotential changes and the generation of force by the muscle, power should be applied roughly from before B, through C, and nearly to D in Fig. 32. The contraction could certainly be overpowered by the *M. subclavius* during any of the powered phase of the jump, although the quiescence before and after D indicates probable shoulder joint depression late in the jump. The jump on which electromyographic data are available did not lead to flight (the bat landed on the side of the flight chamber after the jump). Thus, the flick and subsequent first downstroke do not occur and the contraction to

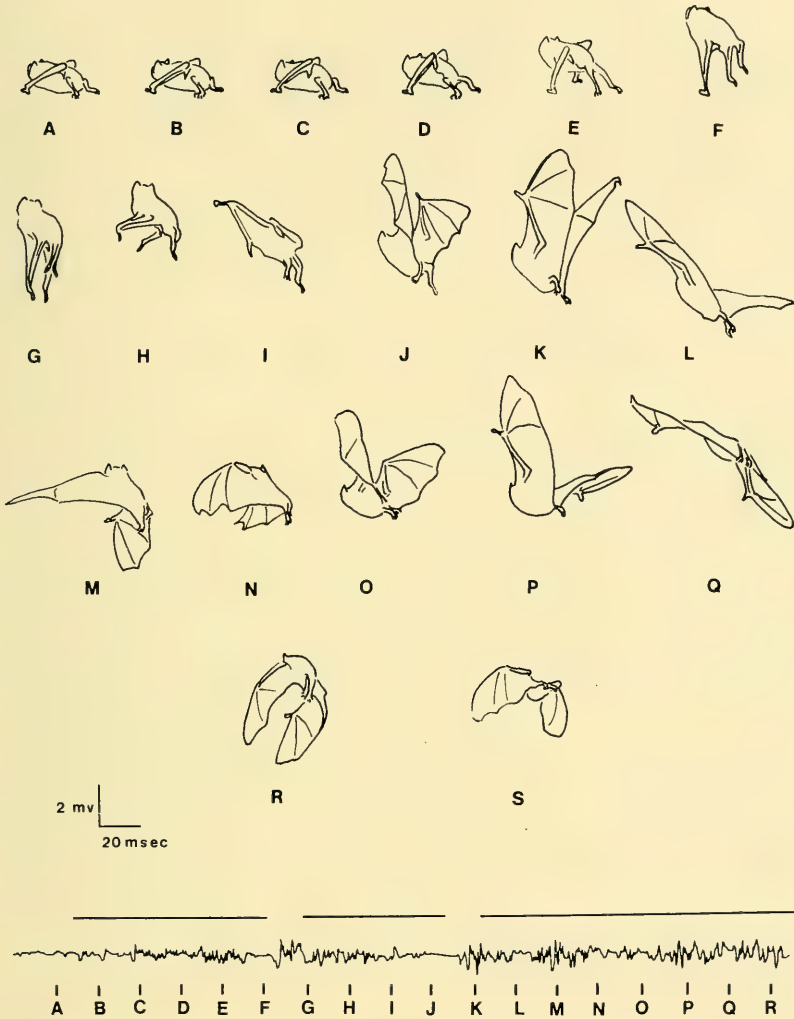


FIG. 33. Electromyogram of right *M. spinotrapezius* of *Desmodus* and corresponding locomotor behavior. The contraction of the muscle occurs slightly after the electrical event and is shown as a solid line above the electromyographic recording. Corresponding locomotor stages and portions of the electromyogram are indicated by the same letters.

raise the clavicle and shoulder from the adducted position is not seen. A short burst of activity after the powered phase of the jump might be the beginning of such a contraction.

M. acromiotrapezius (Fig. 42).—The origin is on the dorsal midline from the posterior tip of the tubercle on the first thoracic vertebra to the posterior tip of the fifth thoracic vertebra. Insertion is onto the tendon of origin of the *M. acromiodeltoideus* from a point about half a millimeter anterior to the tip of the acromial process and posteriorly for 7.5 mm along the lateral aspect of the acromial process and scapular spine.

The anterior portion of the acromiotrapezius, which inserts on the enlarged area of the acromion process, is three times as thick as any portion posterior to it. The combined clavotrapezius and acromiotrapezius is thicker anteriorly in many other bats (Vaughan, 1959; Norberg, 1970*b*), but the thickened anterior portion is usually considered the *M. clavotrapezius*. In *Desmodus*, the thick anterior portion is suited to powerfully tip the acromial process mediad and thus the medial scapular border ventrad, independent of movement of the clavicle. As Vaughan (1959) noted, this action can initiate abduction of the humerus when the latter is locked with the ventral scapular border. In addition, this muscle probably helps steady the scapula when the bat is moving on the ground and the lateral scapular border is tipped strongly ventrally.

M. spinotrapezius (Fig. 42).—Origin is on the dorsal midline from the eighth thoracic vertebra to the posterior tip of the second lumbar vertebra. Insertion is from the dorsolateral aspect of the thickening at the junction of the spine and medial scapular border to a point about 5 mm anterior.

As in other bats (Vaughan, 1959; Norberg, 1970*b*), this muscle is situated to exert a strong posterior pull on the medial scapular border. This is important, because the fulcrum of scapular motion is the anterior articulation with the clavicle. A posterior anchor is necessary if the muscles applying ventral force to the medial and lateral scapular borders are to be effective in rocking the scapula and the wing when the humerus and scapular border are locked. Assuming a 10 millisecond temporal delay, electromyographic data illustrate continuous, probably moderate, contraction during the jump and quiescence at its end (Fig. 33A–F). Activity during the coasting phase may reflect initial limb abduction and scapular stabilization (Fig. 33G–J), but it is much better positioned for the

latter. However, the relatively great activity around G suggests this muscle may be important in reorienting the scapula after its lateral border is so highly depressed during the jump. The posteriorly elongate scapula in this species is a feature that aids scapular stabilization by the *M. spinotrapezius* during movements in flight and terrestrial locomotion. Function in the former role is suggested by nearly continuous activity during the next two wingbeats (Fig. 33K–R).

Costo-spino-scapular Group

M. levator scapulae (Fig. 42).—The origin of this muscle is by four slips onto the dorsal projections of the transverse processes of the fourth through seventh cervical vertebrae. Insertion is on the medial scapular border, beginning about 5 mm posterior to the anterior tip of the scapular flange and continuing posteriorly to the junction of the spine and medial border.

As in other bats (Vaughan, 1959; Norberg, 1970*b*), this muscle tips the medial scapula border ventrad and, along with the *M. acromiotrapezius* and the anterior division of the *M. serratus anterior*, can brace the scapula or aid in the upstroke. The deep, ventral arch of the cervical vertebrae and the relatively high position of the scapula separate the origin and insertion of this muscle more than in most bats and allow it to exert nearly constant force, irrespective of the position of the scapula.

M. serratus anterior, anterior division (Figs. 42, 45).—The origin of the muscle is by two large bellies: one from the anterior face of the first rib adjacent to its articulation with the first costal cartilage, and the other by a slip from a tubercle lateral to the transverse foramen of the sixth cervical vertebra and a slip from a tubercle ventral to the dorsal projection on the transverse process of the seventh cervical vertebra. Insertion is onto the medial scapular border from the anterior tip of the flange posteriorly to within about 4 to 5 mm of the junction of the spine and medial border.

The anterior portion of the serratus, anterior division, is thick; the posterior portion is thin and membranous. Thus, most of the contractile force is exerted on the enlarged scapular flange and tilts the medial border ventrad. Along with the *M. levator scapulae*, *M. acromiotrapezius*, and *M. rhomboideus*, this muscle aids in abduction of the arm when the humerus is locked ventrally with the

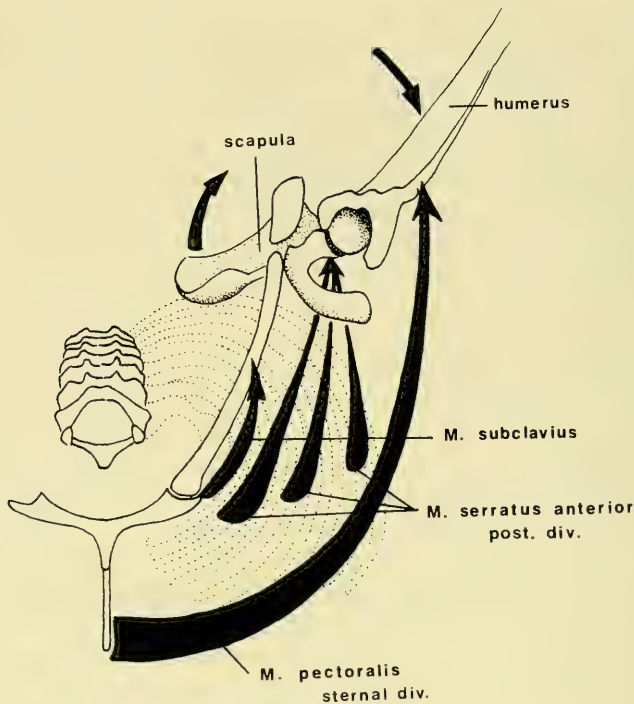


FIG. 34. Diagram of anterior view of the rib cage, pectoral girdle, and proximal end of the humerus of *Desmodus* showing primary adductive forces during the powered phase of a jump or during the downstroke in initial flight following a jump. The humerus is dorsally locked with the scapular border.

lateral scapular border and probably steadies the scapula during jumping behavior and terrestrial locomotion.

M. serratus anterior, posterior division (Figs. 34, 42, 44–45).—The origin extends from the lateral aspect of the first costal cartilage in a line along the junctions of the second through sixth ribs and their costal cartilages, then dorsally along the costal cartilages of ribs seven and eight to the level of the junction of rib eight and its costal cartilage. Insertion is on the lateral and ventral aspect of the lateral scapular border, from the posterior tip of the posterior cartilaginous extension anteriorly to within about 3 mm of the glenoid fossa.

As in other bats (Macalister, 1872; Vaughan, 1959; Norberg,

1970b), the posterior division of the serratus is massive. When the humerus is locked with the dorsal scapular border, this muscle can adduct the brachium, as in the first portion of the downstroke or in much of the powered phase of the jump (Fig. 34). A tremendous amount of power is required in the jump to accelerate the bat upward with a heavy load of blood. This muscle is probably able to assist the sternal *M. pectoralis* in this movement through an arc of more than 130 degrees.

The posterior division of the *M. serratus anterior* also is vital in the first of the downstroke where it assists the *M. pectoralis* in adducting the extended wing, as described by Vaughan (1959) in other bats. Following a jump, air speed is low and the first few wingbeats must rapidly accelerate the bat. By functioning simultaneously in the first half of the downstroke, the posterior division of the *M. serratus anterior* and the *M. pectoralis* supply maximal power to the wing when it is configured to provide both thrust and lift. During faster and more efficient flight, a division of labor, suggested by Vaughan (1959) for other species of bats, between the *M. serratus anterior*, *M. pectoralis*, and *M. subscapularis* may occur and the muscles may not contract simultaneously.

During terrestrial locomotion, forces acting on the pectoral limb are transferred to the lateral scapular border by the humerus. During locomotion with the body extremely elevated, as seen in terrestrial feeding behavior, this muscle tips the short axis of the scapula nearly vertically, thus directing the forces acting against the pectoral limbs directly upward against the scapula, with little or no rotational component. The *M. serratus anterior* and the clavicle thus act as a sling to support the body.

M. rhomboideus (Fig. 42).—The origin is a large belly from thoracic vertebrae one through six; a small anterior slip on the tendinous sheet that is the origin of the *M. clavotrapezius*; and a third slip on the dorsal spinal musculature adjacent the first thoracic vertebra. Insertion is on the ventral and medial aspect of the posterior cartilaginous extension of the scapula and anteriorly along the medial scapular border to its junction with the scapular spine.

Thin anteriorly, the rhomboideus becomes thick posteriorly in the region of its insertion on the posterior cartilaginous extension of the scapula. This suggests the major function is to shift the scapula anteriorly and tilt its medial border ventrad. As in other bats (Vaughan, 1959; Norberg, 1970b), this muscle functions with

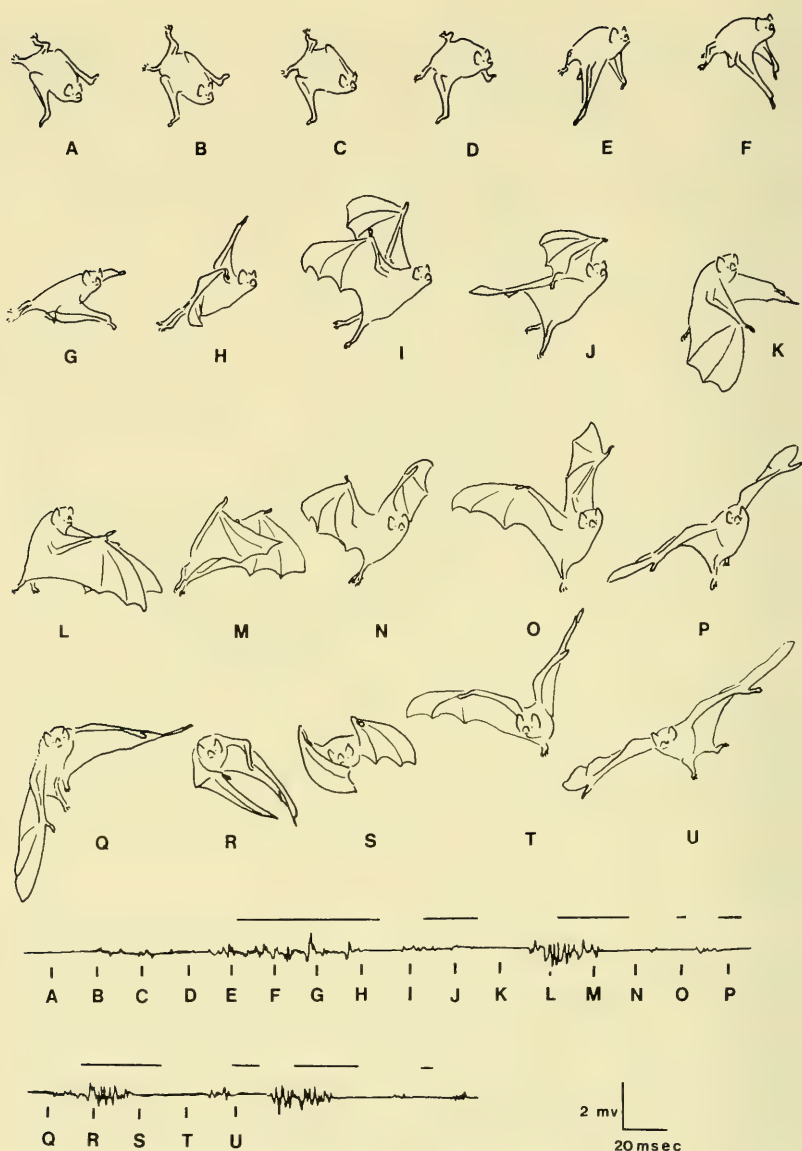


FIG. 35. Electromyogram of right *M. latissimus dorsi* of *Desmodus* and corresponding locomotor behavior. The contraction of the muscle occurs slightly after the electrical event and is shown as a solid line above the electromyographic recording. Corresponding locomotor stages and portions of the electromyogram are indicated by the same letters.

the *M. acromiotrapezius*, *M. levator scapulae*, and the anterior division of the *M. serratus anterior* to power the initial abduction of the arm or to steady the scapula when contracting against the antagonistic posterior division of the *M. serratus anterior*. Anteroposterior movements of the scapula probably aid in balancing the bat over the line of force exerted by the pectoral limbs during a jump and in stabilizing the shoulder girdle during turning maneuvers (Fig. 18).

M. omocervicalis (Fig. 42).—Origin is on the ventral arch of the atlas. Insertion is onto the dorsal border of the clavicle and half a millimeter of the adjacent *M. subclavius*, 7 mm distal to the sternal articulation of the clavicle.

The omocervicalis probably aids in the movement of the head. Insertion on the central clavicle instead of the acromial process (as in many other bats) is indicative of the great motility of the head in this species.

Latissimus-subscapular Group

M. latissimus dorsi (Fig. 42).—Origin is on the dorsal midline from the posterior tip of thoracic vertebra nine to the anterior tip of lumbar vertebra three. Insertion is in common with the *M. teres major* on the low ridge on the ventral aspect of the humerus beginning about 3.5 mm distal to the tip of the lesser tuberosity.

The latissimus dorsi and the teres major are well suited to pronate the humerus and thus the entire arm, as well as to flex and abduct the humerus. These movements are important in terrestrial locomotion when the pectoral limbs are pulled posteriad and pronated in the power stroke. Figure 35 illustrates the function of this muscle during a jump into flight and the initial two wingbeats. A 10 millisecond temporal delay between myopotential changes and contraction is assumed. Contraction begins at the onset of the coasting phase (Fig. 35E) and probably helps abduct the wing. During the early part of the initial flick (Fig. 35H), contraction helps pronate the arm to drive the digits upward and backward against the airstream and help position the wing for the first downstroke. Slight electrical activity indicates weak contractions during the downstroke that perhaps help stabilize the angle of attack and may reinforce the strong pronation of the wing. After flexion and supination of the arm in the first of the upstroke, sudden contraction helps pronate and abduct the arm early in the flick phase (Fig. 35L to between M and N). This myopotential burst indicates

strong, perhaps maximal, contractive force during this movement. Feeble contractions again occur periodically during the downstroke, perhaps for fine control of wing orientation, and a strong contraction occurs early in the flick phase (Fig. 35R to between S and T).

M. teres major (Fig. 42).—Origin is on the lateral scapular border from the level of the junction of the spine and medial border to within about a millimeter of the posterior tip. Insertion is with the *M. latissimus dorsi* on the ventral aspect of the humerus distal to the lesser tuberosity.

The function of the teres major is essentially similar to that of the *M. latissimus dorsi*, except that it is not suited to abduct the humerus. It probably functions primarily in the flick phase of the upstroke in flight, in terrestrial locomotion, and in climbing.

M. subscapularis (Fig. 45).—Origin is on the ventral aspect of the scapula and posterior cartilaginous extension to within 2 mm of the base of the coracoid process and within 2 mm of the posterior edge of the glenoid fossa. Insertion is onto the posterior and medial aspect of the tip of the lesser tuberosity of the humerus.

Although no electromyographic data are available, the subscapularis almost certainly functions to adduct the humerus after it is unlocked from the dorsal scapular border in the last of the downstroke in forward flight, as described by Vaughan (1959). In an alighting maneuver (Fig. 23), the subscapularis, along with the clavicular *M. pectoralis*, extends and adducts the humerus prior to contact of the substrate by the forelimbs and probably helps cushion the impact by contraction as the humerus is forced upward and backward.

Deltoid Group

M. clavodeltoideus (Figs. 42, 44).—Origin of a large belly is from the anterodorsal aspect of the clavicle for about 9 mm beginning approximately 2.5 mm from its distal tip; and a small belly, deep to the first, from about 2 mm of the anteroventral surface of the clavicle in the region of the sharp posterior curve of the clavicle before its articulation from the scapula. Insertion of the larger belly is onto the anterior aspect of the expanded proximal tip of the pectoral ridge and laterally for 9 mm. The second belly inserts onto the dorsomedial aspect of the proximal end of the pectoral

ridge and onto a ridge on the anterior base of the greater tuberosity.

Both bellies are clearly separate from the clavicular portion of the *M. pectoralis*. The clavodeltoideus powers the forward, recovery stroke of the brachium during terrestrial locomotion and the thrusting stroke of the brachium during backward climbing. It is probably aided in this movement by the clavicular *M. pectoralis* and somewhat by the *M. subscapularis*. Its clear separation from the clavicular *M. pectoralis* suggests that the clavodeltoideus is important in powering the complex movements of terrestrial locomotion and climbing.

The clavodeltoideus cannot assist in adduction of the brachium during the powered phase of the jump or in the downstroke of forward flight, but it is important in controlling the angle through which adduction progresses. Steady contraction during a downstroke would direct the stroke strongly forward. In a braking maneuver, this muscle functions to anteriorly brace the wing as it remains extended at a high angle of attack.

M. acromiodeltoideus (Fig. 42).—The origin is on the tendon of insertion of the *M. acromiotrapezius* at a point anterior to the acromion process and extending for 6 mm along the lateral aspect of the acromion process and scapular spine. Insertion is on the anterior 2 mm of the dorsal aspect of the pectoral ridge beginning 5 mm distal to the tip of the greater tuberosity and continuing lateral for 11 mm.

The acromiodeltoideus is situated to abduct, slightly flex, and impart a strong supinating force to the humerus. The relatively long scapula, along with bracing supplied by the *M. spinotrapezius*, provides a stable origin for the muscle to supinate the brachium and thus raise the wing when the forearm is flexed toward the brachium, as occurs at the beginning of the upstroke. An electromyographic record during a jump and initial flight indicates a relatively long contraction during the adduction of the brachium (Fig. 36D–G). This seems surprising, but possibly the acromiodeltoideus stabilizes the dorsal locking of the scapula and humerus throughout the entire powered phase of the jump, thus suggesting that the humerus is not adducted relative to the scapula during even the last of the jump. The posterior division of the *M. serratus anterior* and the sternal *M. pectoralis* thus would supply the power for the entire adduction of the brachium. The relatively free ar-

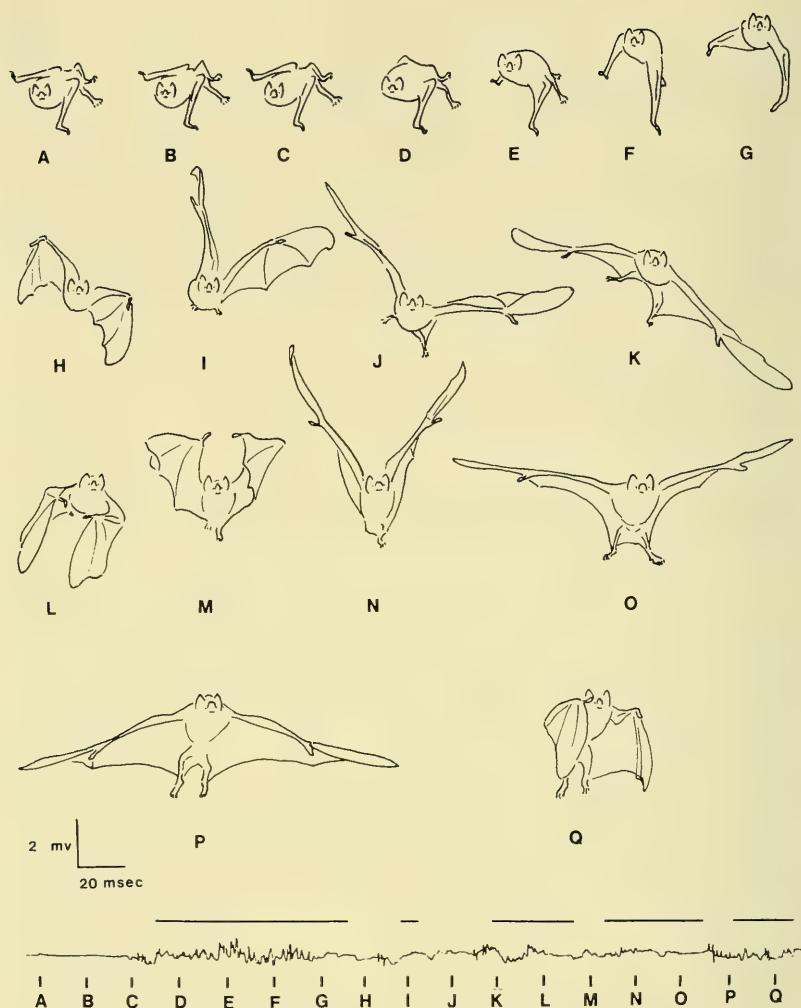


FIG. 36. Electromyogram of right *M. acromiodeltoideus* of *Desmodus* and corresponding locomotor behavior. The contraction of the muscle occurs slightly after the electrical event and is shown as a solid line above the electromyographic recording. Corresponding locomotor stages and portions of the electromyogram are indicated by the same letters.

ticulation of the scapula and clavicle allows the two largest muscles in the bat to power the adduction of the brachium during the jump. The *M. subscapularis* apparently does not aid the adduction during the jump as perhaps it does in the downstroke of forward flight, as Vaughan (1959) suggested for other bats. However, the electromyographic data provide no evidence that the *M. subscapularis* does not overpower the deltoid group and adduct the humerus relative to the scapula at the very last of the powered phase of the jump.

Contraction of the *M. acromiodeltoideus* probably continues during the first part of the coasting phase of the jump, or until the initiation of the flick phase (Fig. 36, between G and H). Activity depicted at Fig. 36I suggests the muscle again stabilizes the dorsal locking of scapula and humerus prior to the downstroke. Only slight activity is apparent in the first downstroke, but contraction again occurs at the last of the downstroke and onset of the upstroke, and continues to the initiation of the flick phase (Fig. 36, K to between L and M). Contraction at the end of the upstroke again indicates stabilization of dorsal locking of scapula and humerus. The muscle probably functions to supinate and abduct the brachium during the very last of the downstroke and first half of the upstroke. Final positioning of the brachium prior to the downstroke appears to be the function of the *M. latissimus dorsi* and *M. teres major*.

M. spinodeltoideus (Fig. 42).—Origin is by a tendinous raphe over the scapular spine and then along the dorsal aspect of the thickened medial scapular border to its posterior tip. Insertion is by a flat tendon posterior to the proximal 2.5 mm of the insertion of the *M. acromiodeltoideus*.

The spinodeltoideus is relatively thin and situated to slightly abduct, flex, and supinate the humerus. An electromyographic recording during a jump into flight (Fig. 37) illustrates contractions similar to those of the *M. acromiodeltoideus* (Fig. 36). Initially, there is a contraction that, along with the other deltoid muscles, probably stabilizes the locking of the humerus and dorsal scapular border. The contraction continues during the powered phase of the jump, but becomes less intense over the last half of the adduction of the brachium (Fig. 37F). At the beginning of the coasting phase (Fig. 37G), contraction aids the supination and perhaps the abduction of the brachium. In the flick phase, slight contraction apparently

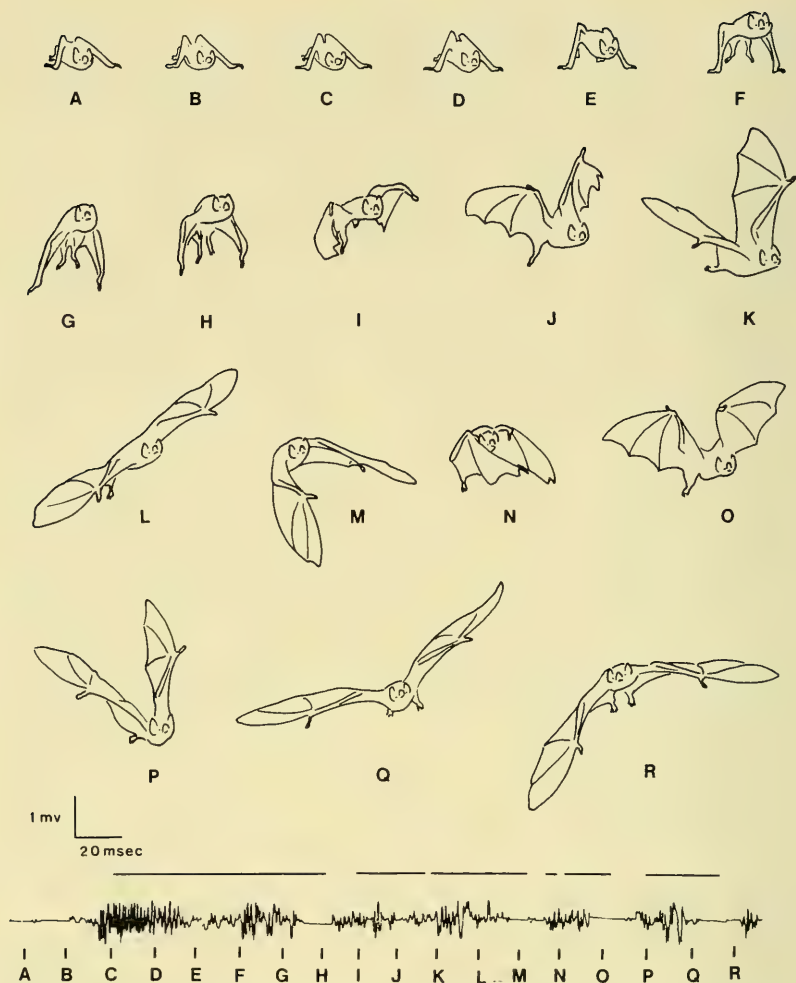


FIG. 37. Electromyogram of right *M. spinodeltoideus* of *Desmodus* and corresponding locomotor behavior. The contraction of the muscle occurs slightly after the electrical event and is shown as a solid line above the electromyographic recording. Corresponding locomotor stages and portions of the electromyogram are indicated by the same letters.

helps pull the brachium mediad prior to the downstroke (Fig. 37I–J). The supinating force imparted by this contraction is probably offset by the pronating force of the *M. latissimus dorsi*, *M. teres major*, and *M. pectoralis*. With the wing at the level of midbody, another contraction occurs that probably tends to reduce some of the pronation imparted by the *M. pectoralis* and conforms the wing into more of a lift-generating structure (Fig. 37K to between L and M). As the humerus probably is locked with the dorsal scapular border at this point, this contraction does not detract from the adductive forces applied to the brachium. The contraction continues into the first phase of the upstroke to help supinate the wing and again in the flick phase to position the brachium for the downstroke. Another contraction early in the downstroke (Fig. 37P–Q) probably reinforces the scapulo-humeral locking and stabilizes the arm against some of the pronating force applied by the *M. pectoralis*.

M. teres minor.—The origin is on the posterodorsal aspect of the rim of the glenoid fossa and onto the tendon of origin of the long head of the *M. triceps brachii*. Insertion is on the dorsal surface of the greater tuberosity of the humerus for 1.5 mm distal to the insertion of the *M. infraspinatus*. The small teres minor is a weak supinator and flexor of the humerus.

Suprascapular Group

M. supraspinatus (Fig. 42).—The origin is from the medial 3 mm of the supraspinous fossa and adjacent ligamentous raphe over the scapular spine, and from the dorsolateral aspect of the scapular flange. Insertion is by a heavy tendon onto a groove on the medial surface of the greater tuberosity of the humerus.

As in other bats (Vaughan, 1959; Norberg, 1970b), the supraspinatus abducts, slightly supinates, and extends the humerus. Along with some of the deltoid group (Figs. 36–37), it probably stabilizes the dorsal locking of the scapula and humerus and helps abduct the humerus relative to the scapula during the upstroke in forward flight. In terrestrial locomotion, it is best suited to swing the humerus forward and, by supinating and slightly abducting the humerus, to lift the carpus off the substrate for the forward swing. In terrestrial feeding postures, when the short axis of the scapula is oriented nearly vertically, this muscle, along with the *M.*

infraspinatus and *M. subscapularis*, is important in moving the pectoral limb.

M. infraspinatus (Fig. 42).—Origin is from the lateral aspect of the scapular spine; lateral aspect of the medial border posterior to the spine; dorsal base of the posterior caritilaginous extension; medial aspect of the lateral border to within 3 mm of the origin of the *M. triceps brachii*, long head; and surfaces of the three facets (Fig. 26). Insertion is by a thick tendon, a millimeter wide, onto the dorsal aspect of the tip of the greater tuberosity of the humerus.

The posteriorly elongate scapula in *Desmodus* positions the origin of the infraspinatus relatively far posterior to the insertion. The insertion on the dorsal aspect of the greater tuberosity also is displaced well above the fulcrum at the center of the head. Thus this muscle is the most powerful supinator of the brachium and no doubt functions in the last part of the downstroke and first part of the upstroke to raise the forearm and hand anteriorly to the body. As this muscle is not situated to provide much abductive force to the humerus, it is probably relatively important in the last half of the downstroke in counteracting the pronating forces applied by the *M. pectoralis*, and helps position the wing into a lift-generating configuration (Fig. 19).

Triceps Group

M. triceps brachii, caput lateralis (Fig. 43).—The origin is from a strip a millimeter wide along the posterior surface of the humerus beginning at the base of the lesser tuberosity and extending dorsally to the level of the top of the head. Insertion is by a large sesamoid onto the olecranon process of the ulna.

M. triceps brachii, caput medialis (Fig. 43).—The origin extends over 13 mm of the posterodorsal surface of the humerus beginning 2 mm lateral to the head. A second group of short fibers, assumed to be part of this head, originates along the posterior aspect of the distal half of the humerus and inserts into the common tendon to the olecranon process of the ulna. Insertion is by a large sesamoid onto the olecranon process of the ulna.

M. triceps brachii, caput longus (Fig. 43).—Origin is by two slips from the two tubercles, 1.5 mm apart, posterior to the posterior border of the glenoid fossa of the scapula. Insertion is by a large sesamoid onto the olecranon process of the ulna.

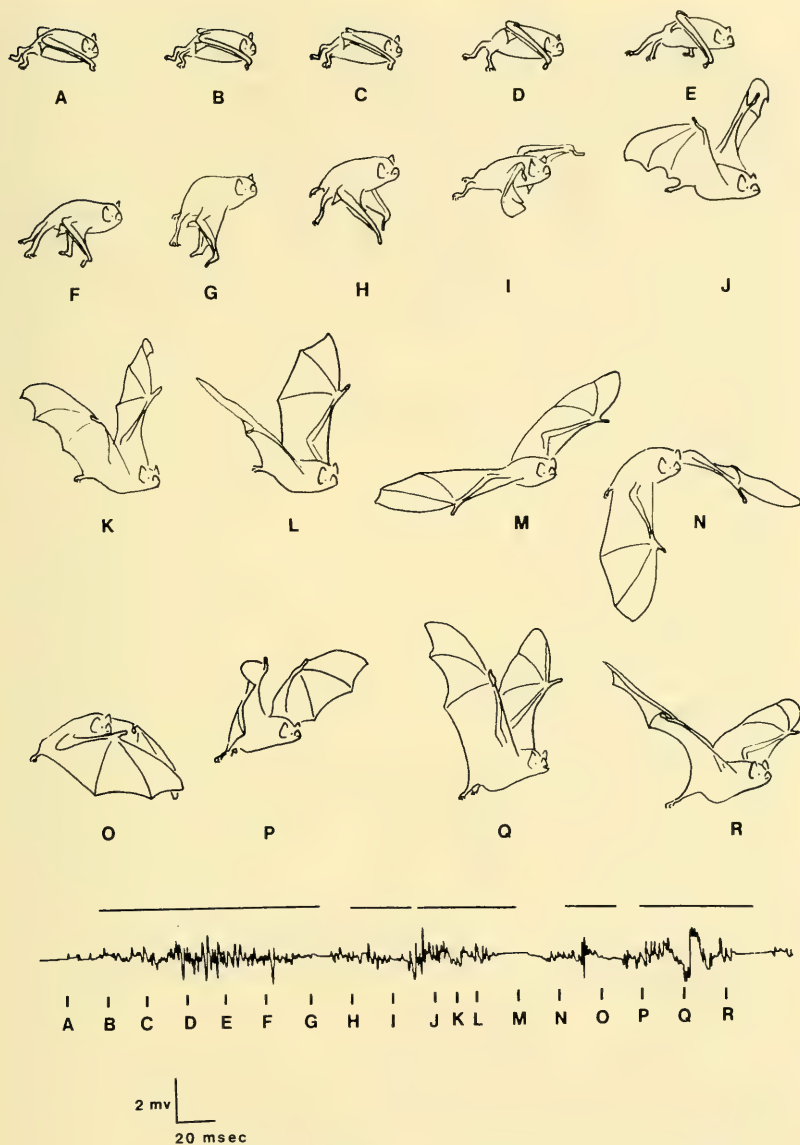


FIG. 38. Electromyogram of right *M. triceps brachii*, long head, of *Desmodus* and corresponding locomotor behavior. The contraction of the muscle occurs slightly after the electrical event and is shown as a solid line above the electromyographic recording. Corresponding locomotor stages and portions of the myogram are indicated by the same letters.

An electromyographic record of the long head of the triceps muscle during a jump into forward flight reveals a contraction that begins during the inclination of the brachium and continues until contact with the substrate is broken (Fig. 38B–G). After only a short period of quiescence during the first of the coasting phase (Fig. 38G–H) when contraction of the *M. biceps brachii* flexes and begins supination of the forearm (Fig. 40G–H), contraction begins to extend the forearm (Fig. 38H–I). The electromyogram shows an increase in amplitude that probably represents greater strength of contraction during the flick phase (Fig. 38I–K), where the forearm is fully extended along with the digits to provide forward thrust and to help position the wing for the first downstroke. The contraction continues during the first half of the downstroke and maintains the full extension of the arm (Fig. 38K–M). Past the level of midbody, contraction ceases and the *M. biceps brachii* (Fig. 40L–N) begins flexion of the forearm that continues through the first third of the upstroke. Contraction of the triceps begins at about the second third of the upstroke, stops for a few milliseconds, and then continues during the flick phase and the first half of the next downstroke (Fig. 38O–R).

Although the electrodes were in the long head of the triceps, one of the leads was near (and possibly may have contacted) the posterodorsal aspect of the lateral head, and may have monitored some of its electrical activity. Although the function of the three heads may be slightly different, the nearly inseparable contact of the bellies, the close approximation of the origin of the long, lateral, and most of the medial head, and their common insertion on the olecranon process, suggest that their action is functionally and temporally quite similar. The long head may function to slightly flex the brachium but, because the mechanical advantage is poor for this movement, it could be easily counteracted by the scapular musculature.

The large sesamoid in the insertional tendon is contoured to fit closely the concavity on the posterior side of the distal articular surface of the humerus and suggests that considerable tension is applied by this muscle group. The jump is certainly the most demanding of the triceps, as it is the third largest muscle powering the jump and since it must move the forearm through an arc of about 140 degrees.

Extensor Group of the Forearm

M. extensor carpi radialis brevis (Figs. 46, 48).—The origin is by a tough tendon on the medial edge of the dorsal epicondyle of the humerus. Insertion is on a large tubercle on the anterodorsal base of metacarpal III by a heavy tendon and onto the dorsolateral tip of the trapezium by a rather elastic band of connective tissue.

By extending the third digit, this muscle extends the fifth digit and aids the *M. extensor carpi radialis longus* in extending the remainder of the hand-wing. A detailed discussion of both muscles is included with the discussion of the *M. extensor carpi radialis longus* below.

M. extensor carpi radialis longus (Figs. 46–48).—Origin is by a heavy tendon on the medial aspect of the dorsal epicondyle of the humerus. Insertion is onto the anterodorsal base of metacarpal II and into a depression in the lateral base of metacarpal I by a heavy tendon.

In *Desmodus*, as in other species of bats (Vaughan, 1959; Norberg, 1970b), this muscle and the adjacent *M. extensor carpi radialis brevis* are the largest muscles in the forearm. Although their origins are displaced mediad to the center of rotation of the elbow joint, the extremely large size of the bellies and the lack of a tough connective tissue covering found in many other bats suggests that these muscles are well suited to act independently of movements at the elbow. Vaughan (1959) pointed out that in other species of bats, such as *Eumops perotis*, *Myotis velifer*, and *Macrotus waterhousii*, these muscles can act as relatively inelastic bands and automatically extend the chiropatagium as the elbow is extended. This helps concentrate the weight toward the body and eliminate weight in the wing. The terrestrial propensity of *Desmodus*, and particularly its jumping behavior, necessitate complete independence of movements of the hand from movements of the rest of the arm, although there appears to be a sacrifice of added weight in the wing. The muscles are certainly stretched by extension of the elbow, but the elastic components appear to absorb this movement and allow the hand to remain folded against the forearm. This feature may help explain the strong and mechanically advantageous insertion of some of the flexors of the hand that have to hold the hand flexed while the arm is fully extended, as in terrestrial feeding

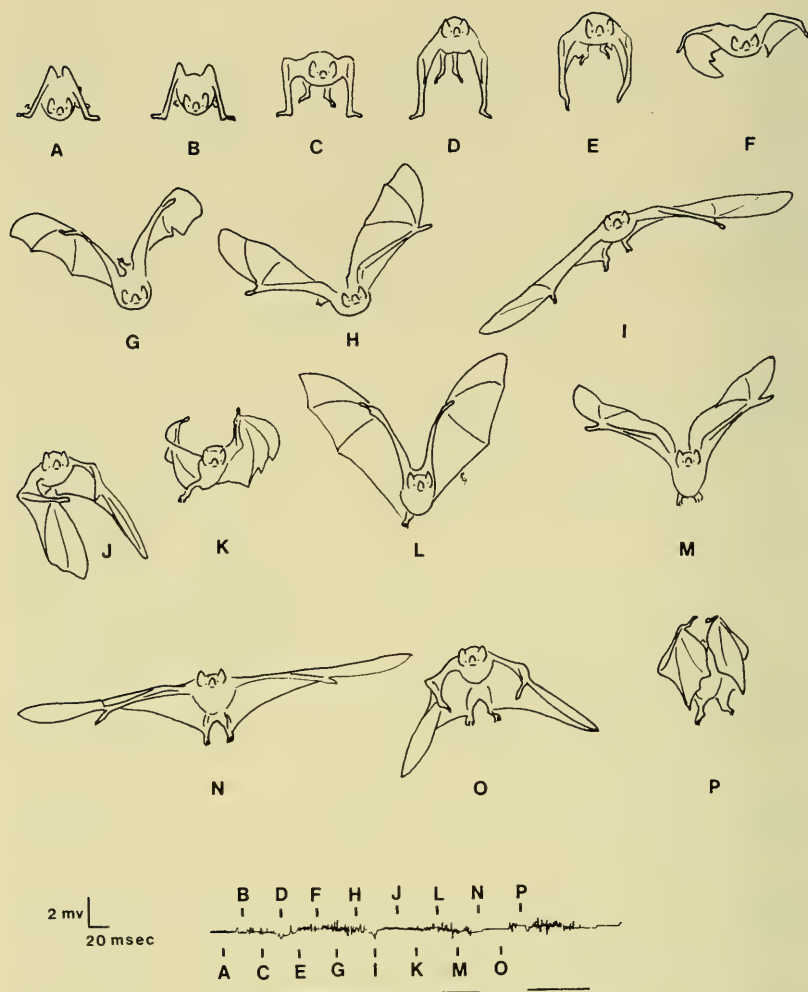


FIG. 39. Electromyogram of right *M. extensor carpi radialis longus* of *Desmodus* and corresponding locomotor behavior. The contraction of the muscle occurs slightly after the electrical event and is shown as a solid line above the electromyographic recording. Corresponding locomotor stages and portions of the myogram are indicated by the same letters.

posture or in the powered phase of the jump. This muscle begins contraction during the powered phase of the jump and continues until late in the first downstroke (Fig. 39, B to between I and J). Shortly after the start of the coasting phase (Fig. 39E), partial extension of the digits is evident; however, I cannot fully explain the early initiation of contraction. Perhaps co-contraction of antagonists tends to brace the carpus as the thrust of the pectoral limb is directed against it and the thumb. The greater number of spikes in the electromyogram indicate that the contraction during the flick phase is stronger than that before it, suggesting that perhaps the movement meets considerable resistance.

The muscle is quiescent in the last of the downstroke and first half of the upstroke (Fig. 39I–K), but contracts during the last of the flick phase and through the first half of the next downstroke (Fig. 39, between K and L–N). The sequence of contraction is essentially similar during the last of this cycle as in the one preceding it. Although no electromyographic data are available for the *M. extensor carpi radialis brevis*, I assume its function is similar to that of the *M. extensor carpi radialis longus*.

M. supinator (Fig. 46).—Origin is by a heavy tendon onto the center of the dorsal (lateral) epicondyle of the humerus. Insertion is over 10 mm of the anterior surface of the radius beginning 3 mm distal to its proximal articular surface.

As in other bats, this muscle originates by a tendon that contains a sesamoid bone and is a flexor of the forearm. The muscle lacks good mechanical advantage for this action. Thus it probably functions mainly to brace and stabilize the elbow joints as strong supinating forces, applied proximally to the humerus, raise the flexed forearm as in the first half of the upstroke (Fig. 20). The relatively large size of this muscle suggests the importance of this function.

M. extensor pollicis brevis (Fig. 48).—Origin is along 10 mm of the interosseous surface of the ulna beginning 3 mm distal to the tip of the olecranon process. Insertion is by a tendon heavily bound to the anterodorsal aspect of the carpus and metacarpal I, which attaches on the dorsal aspect of the proximal base of the first phalanx of digit I.

This muscle extends the thumb and, if resisted by the flexors of the first metacarpal, extends the phalanges of the thumb. *Desmodus* commonly rests much of its weight on the distal pad at the meta-

carpophalangeal junction of digit I during terrestrial locomotion or when standing (Fig. 2), and this muscle is necessary in elevating the claw during movements of the limb from this position. When *Desmodus* is walking on a nervous or easily aroused host animal prior to feeding, the claws may be elevated to minimize stimulation of the skin of the host.

M. abductor pollicis longus (Fig. 49).—Origin is on 7 mm of the interosseus surface of the ulna and along 16 mm of the interosseus surface of the radius beginning at the medial contact of the radius and ulna. Insertion is by a thick tendon on the anterior tip of the scaphoid. The tendon divides proximal to the scaphoid and another branch runs forward, inserts onto the ventromedial sesamoid on the distal tip of metacarpal I, and sends fibers into the pad at the metacarpophalangeal joint of digit I.

The tendon, which inserts on digit I, probably is the remnant of the *M. abductor pollicis brevis*, which has become tendinous and shifted its origin from the scaphoid directly to the tendon of the *M. abductor pollicis longus*. No doubt the elongation of the first digit in *Desmodus* and its use in jumping have necessitated the reduction of the *M. abductor pollicis brevis* to a tendon. The large and relatively long belly of the *M. abductor pollicis longus* on the forearm is better suited to provide power through a wide arc of movement than is a shorter and much smaller muscle originating on the hand. By becoming tendinous and shifting its origin directly to the tendon of the *M. abductor pollicis longus*, the *M. abductor pollicis brevis* allows more powerful movement of the thumb. Although no electromyographic data are available, it is evident that the *M. abductor pollicis longus* serves two important functions. Its contraction pulls the scaphoid mediad over the lunar and thus puts tension on the *M. abductor digiti quinti* (Fig. 49), which originates from the scaphoid, and puts tension on the pisiform itself. As Vaughan (1959) noted, this is important in bracing the fifth metacarpal and basal phalanx of digit V against upward deflection during adduction of the wing. In addition, the *M. abductor pollicis longus* pulls the first metacarpal ventrad and is important in terrestrial locomotion. In terrestrial feeding postures, or in terrestrial locomotion with the body held high above the substrate, this muscle shifts the weight from the basal to the distal thumb pad thus elevating the bat higher. Contraction also aids in keeping the wing folded by flexing the fifth digit through tension on the *M. abductor digiti quinti*. During the

last of the power phase of the jump, the *M. abductor pollicis longus*, along with the *M. flexor digitorum profundus* and *M. palmaris longus*, pull the thumb ventrad to provide the last upward thrust. In addition, all of these muscles produce flexion of at least one digit besides the first, thus helping to keep the remainder of the hand folded.

M. extensor digiti quinti proprius (Fig. 48).—Origin is by a thin tendon onto the distal edge of the dorsal (lateral) epicondyle of the humerus. Insertion is onto the dorsal aspect of the proximal tip of the second phalanx of digit V by a broad tendon.

At the point where this tendon meets the dorsal surface of the fifth metacarpal, it is joined by a small tendon of the *M. extensor digitorum communis*. This muscle deflects the phalanges of digit V upward and tends to elevate the metacarpal slightly. The relative size of the belly and the insertional tendon suggest this movement is important. High-speed photographs of *Desmodus* in flight (Fig. 19) show that during the first half of the downstroke the phalanges of digit V are deflected upward, thus shaping the distal plagiopatagium and medial chiropatagium into a thrust-generating structure similar to that of the distal chiropatagium. Contraction of this muscle, combined with the passive forces from the air pressure, would cause the upward deflection to be greater than that from the air pressure alone and would shape that part of the wing into a more efficient thrusting configuration. Simultaneous contraction of the *M. abductor digiti quinti*, *M. opponens digiti quinti*, and *M. abductor pollicis longus* would overpower the *M. extensor digiti quinti proprius*, flex the phalanges, depress the metacarpal, and stabilize the phalanx against the metacarpal.

M. extensor digitorum communis (Figs. 46, 48).—Origin is by two separate bellies with tendinous origin on the dorsal (lateral) epicondyle of the humerus and fleshy origin beginning 6 mm distal to the proximal tip of the radius, and extending distad along the dorsal surface of the radius for 14 mm. Insertion is through a tendon to digit III, which runs along the dorsal aspect of the metacarpal and sends fibers to the proximal tips of the first and second phalanges. The primary insertion of the tendon is on the postero-dorsal aspect of the proximal tip of phalanx three. The tendon to digit IV inserts on a tubercle on the dorsolateral aspect of phalanx one, 2 mm distal to the proximal base.

The tendon to digit IV divides distal to the carpus and sends a

branch to the tendon of the *M. extensor digiti quinti proprius* at its proximal contact with the metacarpal, thus it aids in dorsal deflection of the phalanges of digit V. The connections to digits III and IV dorsally deflect the phalanges and slightly deflect the metacarpals. In the downstroke in forward flight (Fig. 19), the *M. extensor digitorum communis* probably aids the force of the air stream in the upward deflection of the phalanges to provide the propeller effect and upturned configuration of the distal chiropatagium between digits III and IV, which perhaps function to reduce tip vortices. It also provides downward acceleration of air and lift production in the last of the downstroke. More important, however, is the function of this muscle in the flick phase of the upstroke. During the first of the flick (Fig. 20N-P), when the forearm is extended, the phalanges of digits III to V are deflected ventrally by the force of the air and perhaps by contraction of the flexors of the digits. As the flick nears completion, the phalanges are fully extended to provide the last component of forward thrust and help to position the wing for the downstroke. This movement appears to be partially active and not simply the result of upward air pressure as adduction begins.

M. extensor carpi ulnaris (Figs. 46-49).—Origin is from the deep groove and adjacent ridge on the proximal 6 mm of the postero-ventral surface of the ulna. Insertion is by a heavy tendon on the tubercle on the dorsomedial aspect of metacarpal V, 2 mm distal to its proximal tip.

This muscle is a powerful flexor of digit V and, because of ligaments that join the proximodorsal surfaces of metacarpals III and V, the entire hand-wing. In the distantly related phyllostomatid bat, *Macrotus*, this muscle inserts on metacarpal V but is an extensor. In *Eumops perotis* and *Myotis velifer* (Vaughan, 1959), this muscle inserts on metacarpal III and is a flexor. In *Plecotus auritus* (Norberg, 1970b), the muscle inserts on metacarpal III and is an extensor. The tendon is the thickest one to the hand, and the belly is quite large. When the forearm is extended with the wing folded as in terrestrial feeding postures or in parts of the climbing and walking cycles (Figs. 2, 4, 6), the large *M. extensor carpi radialis longus* and *M. extensor carpi radialis brevis* are stretched and apply some passive, extensive forces to the hand. This muscle is no doubt necessary to resist these forces and keep the wing folded. Inasmuch as the radial extensors of *Desmodus* are not heavily invested in

connective tissue, they are probably rather elastic and thus do not explain the need for the massive tendon of the *M. extensor carpi ulnaris*. However, in landing on the ground, it is critical for the wing to be quickly folded against the forearm to prevent injury to the digits. It is also important for the wing to remain tightly folded during terrestrial locomotion. The insertion seems well suited for effecting such a rapid and powerful movement.

M. extensor indicis (Fig. 48).—Origin is on 14 mm of the postero-dorsal surface of the radius to within about 4 mm of the distal articular surface and on 9 mm of the interosseus surface of the ulna, beginning about 8 mm distal to the proximal articulation of the radius and ulna. Insertion is at several points. At the level of the proximal carpus, the tendon gives rise to a sheet of tendon that inserts on the anterodorsal carpus and dorsomedial aspect of the proximal half of metacarpal I. Another collateral tendon arises from the main tendon and runs to the dorsolateral aspect of the distal third of metacarpal I. The main tendon inserts by way of a sesamoid on a tubercle on the anterodorsal surface of metacarpal II, 3 mm distal to its proximal base. At the level of the sesamoid, small tendinous attachments run from the main tendon posterolaterad to insert on the dorsal aspect of the bases of metacarpals III and IV.

This muscle functions with the *M. extensor carpi radialis longus* and *M. extensor carpi radialis brevis* to extend the hand-wing during the coasting phase of the jump, and during the flick phase and first half of the downstroke in forward flight. The attachments to the dorsal aspect of the third and fourth metacarpals suggest it also is important in bracing the hand against posterior and dorsal air pressure during the flick phase of the upstroke, when the digits are extended and the wing is strongly pronated and abducted. The attachments to the first digit probably help raise it when the hand is flexed by the *M. extensor carpi ulnaris*, as occurs in terrestrial locomotion.

Pectoralis Group

M. subclavius (Figs. 44–45).—Origin is by a fleshy attachment to the ventral aspect of the first costal cartilage adjacent to its attachment to the manubrium and by tendinous attachment to the anterolateral border of the first costal cartilage. Insertion is on the

posteroventral surface of the clavicle from its distal tip to within 2 mm of its articulation with the manubrium.

Because of the relatively free articulation of the clavicle and scapula, this muscle is important in both jumping and flight. Contraction pulls the distal tip of the clavicle ventrad and slightly posteriad, and can effectively brace the clavicle when co-contracting with the *M. clavotrapezius*. Slight dominance of one or the other could swing the clavicle dorsad or ventrad and still stabilize it as a solid fulcrum for movements of the scapula and arm. High-speed photographs of a jump show that the shoulder joint is depressed, and although no direct evidence is available, this movement appears to be partly the result of depression of the tip of the clavicle by this muscle. The electromyographic data for the *M. clavotrapezius* (Fig. 32) indicate contraction during all but the last of the powered phase of the jump, but such contraction is necessary to stabilize the clavicle and could be overpowered by the *M. subclavius*. Seemingly the subclavius is not opposed by the clavotrapezius at the last of the powered phase of the jump and probably depresses the clavicle.

M. pectoralis.—This muscle appears to be divided into three major bellies in *Desmodus*. However, I distinguish only between clavicular and sternal portions, as the clavicular portion is widely separate from the remainder of muscle. As Vaughan (1959) described for other species of bats, I have noted considerable individual variation in the degree of separation and arrangement of the non-clavicular portion and consider it the posterior (sternal) division.

M. pectoralis, anterior (clavicular) division (Fig. 44).—Origin is on the anteroventral aspect of the proximal base of the clavicle and along the anterior and ventral aspect of the proximal half of its shaft. Insertion is from the dorsal aspect of the medial tip of the pectoral ridge, laterally for about 9 mm, superficial to the insertion of the posterior (sternal) division of the *M. pectoralis*.

The clavicular *M. pectoralis* pulls the humerus craniad and adducts and pronates it slightly. This movement is not part of the normal wingbeat cycle or of a jump, but occurs as the limb is positioned prior to alighting on a horizontal surface (Fig. 23) and in backward climbing (Fig. 6). In terrestrial locomotion, this muscle probably functions along with the *M. clavodeltoideus* to swing the humerus forward in the recovery stroke (Fig. 4). When cocontracting with the sternal division of *M. pectoralis*, the clavicular division

can assist in adduction and pronation of the humerus and is probably responsible for much of the cranial inclination of the path of the wing in the last half of the downstroke (Fig. 19).

M. pectoralis, posterior (sternal) division (Fig. 44).—Origin of one belly is on the lateral aspect of the ventral arm of the manubrium, the ventral aspect of the lateral arms to within 2 mm of their distal tips, and the ventrolateral aspect of the posterior arm; that of the other belly is on the ventral aspect of the body of the sternum to within 2 mm of the posterior tip of xiphisternum and on a tendinous raphe over the midline, beginning anteriorly on the tip of the ventral arm of the manubrium and extending posterior to the posterior tip of the body of the sternum. Insertion is onto the ventral half of the anterior face of the proximal end of the pectoral ridge and laterally for 10 mm along the anterior and ventral edge of the pectoral ridge.

The bellies of this massive muscle are the major adductors and pronators of the humerus, and consequently of the arm and hand. The origin over the manubrium, body, and xiphoid process of the sternum makes this muscle effective in moving the humerus through a variety of planes, as Vaughan (1959) pointed out for other species. However, photographic evidence for *Desmodus* in flight indicates that there is relatively little variability in the plane through which the wing is adducted. The heavy wing loading in this species (Hartman, 1963), combined with the proportionally large meals that are consumed (Wimsatt, 1969), seem to have resulted in relatively unvarying wingbeat patterns as opposed to hovering, nectar-feeding species such as *Leptonycteris sanborni* (Altenbach, 1968).

Along with the *M. serratus anterior*, posterior division, the sternal *M. pectoralis* adducts the humerus during the powered phase of the jump. It is doubtful that the angle of the jump is controlled by the *M. pectoralis*, as a jump, particularly when the bat has a full stomach of blood, probably requires contraction of the entire muscle. Variation in the rotation of the humerus during the jump is likely under the control of the *M. subscapularis*, suprascapular group, deltoid group, clavicular *M. pectoralis*, and *M. latissimus dorsi*.

During the wingbeat cycle, the strong pronation of the arm and hand, which orients the wing into a thrusting configuration during the first half of the downstroke, is a result of contraction of the

sternal division of *M. pectoralis*. There is perhaps more variability in the function of this muscle during a wingbeat cycle than in a jump. Greater contraction of specific parts of the muscle mass can vary the degree of pronation and the plane of adduction of the wing. As in a jump, the rotational stability is also controlled by the supraspinatus, infraspinatus, subscapularis, deltoid group, clavicular *M. pectoralis*, and *M. latissimus dorsi*.

In terrestrial locomotion, the sternal *M. pectoralis* probably supports most of the weight directed against the pectoral limbs. When the bat is in elevated walking postures or standing in terrestrial feeding posture with much of the weight probably supported by the clavicle and posterior division of the *M. serratus anterior*, moving the brachium is the task of the clavicular *M. pectoralis*, deltoid group, and *M. latissimus dorsi*. Sudden movements from these postures would seemingly require the power of the sternal *M. pectoralis*.

M. pectoralis abdominalis (Fig. 44).—Origin is on the abdominal fascia beginning 2.5 mm lateral to the midline at the level of the posterior tip of the xiphoid process and extending posterolaterad for roughly 9 mm. Insertion is by a flat tendon, which attaches to the medial 2 mm of the ventral aspect of the pectoral ridge posterior to the insertion of the *M. pectoralis*.

As in other species, the *M. pectoralis abdominalis* is a rotator (pronator) and flexor of the humerus. During the downstroke it can increase pronation to form more of the medial wing into a thrusting attitude or can oppose the supinating force exerted by the *M. biceps brachii*. The pronation during the flick phase is probably aided by this muscle along with the *M. latissimus dorsi* and *M. teres major*.

In terrestrial locomotion, the power stroke of the pectoral limb is probably aided by this muscle as it pronates and flexes the humerus. The forearm is forced downward and posteriad by this movement, thus driving the body forward.

Flexor Group of the Arm

M. coracobrachialis (Fig. 45).—Origin is on the dorsal third of the anterior face of the coracoid process. Insertion is over about 4 mm of the anteroventral surface of the humerus beginning approximately 11 mm lateral to the medial end of the pectoral ridge.

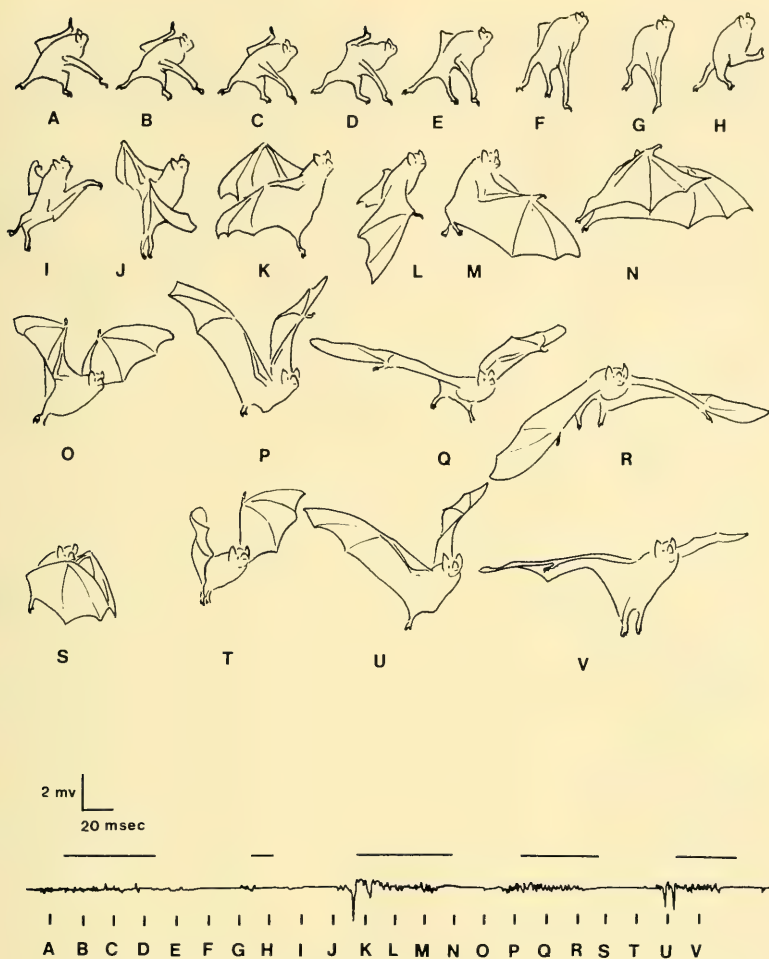


FIG. 40. Electromyogram of right *M. biceps brachii*, coracoid head, of *Desmodus* and corresponding locomotor behavior. The contraction of the muscle occurs slightly after the electrical event and is shown as a solid line above the electromyographic recording. Corresponding locomotor stages and portions of the electromyogram are indicated by the same letters.

The *M. coracobrachialis* is a rather weak adductor and extensor of the humerus. It probably aids in adduction of the wing and exerts a stabilizing force to the brachium.

M. biceps brachii (Figs. 42, 44–47).—The origin of the coracoid

head is on the posterior and lateral aspect of the ventral three-fourths of the tip of the coracoid process. The origin of the glenoid head is by a tough tendon from the tubercle a millimeter anterior to the glenoid fossa on the lateral aspect of the base of the coracoid process. Insertion is by a heavy tendon that runs over the ridge on the proximal end of the radius and attaches into the flexor fossa on the posterior side of the radius.

As in other bats (Vaughan, 1959; Norberg, 1970*b*), the bellies of the biceps are flexors of the forearm and, because of the articulation of the radius and humerus that allows only flexion and extension, supinators of the arm. Electromyographic data from a jump into flight were recorded from electrodes in the coracoid head, but probably are representative of the function of both heads. There is little or no activity during the powered phase of the jump (Fig. 40D–G) and the first contraction is a short burst during the initial part of the coasting phase, which flexes the forearm (Fig. 40G–H). Contraction again begins at the first of the downstroke and continues until the beginning of the flick phase of the upstroke (Fig. 40K–N). When opposed by contraction of the *M. triceps brachii*, the biceps causes adduction of the arm and, as Vaughan (1959) pointed out, provides rotational stability as it opposes the pronating forces applied by the *M. pectoralis*. When the *M. triceps brachii* ceases contraction in the last half of the downstroke (Fig. 38), the biceps flexes and supinates the arm (Fig. 40L–N). The function is similar in the next two cycles (Fig. 40O–V).

M. brachialis (Figs. 46–47).—Origin is over about 9 mm of the anterior face of the humerus beginning 12 mm lateral to the distal end of the pectoral ridge. Insertion is into the flexor fossa of the radius in common with the tendon of the *M. biceps brachii*. This muscle probably assists in the flexion and stabilization of the forearm, as suggested in other species of bats (Vaughan, 1959, 1970*c*; Norberg, 1970*b*). No electromyographic data are available.

Flexor Group of the Forearm

M. flexor carpi ulnaris (Figs. 47, 49).—Origin is on the ventral aspect of the ulna from its medial tip laterally for 5 mm and on the adjacent *M. palmaris longus* about 4 mm distal to its origin. Insertion is onto the posteromedial surface of the pisiform a third of the distance to its ventral tip.

As in several other species of bats (Vaughan, 1959), this is a flexor of the fifth metacarpal and thus the hand, because forces applied to the pisiform are transmitted to the fifth metacarpal. However, the belly is relatively small and the tendon is extremely thin, indicating that the duty of flexion of the fifth metacarpal has been taken over by other muscles such as the *M. extensor carpi ulnaris*. As in *Macrotus* (Vaughan, 1959), the origin allows complete independence of movement at the elbow and facilitates the abduction of the extended hand-wing anterior to the body to provide low drag on the upstroke.

M. palmaris longus (Figs. 47, 49).—Origin is by a heavy tendon on the distal tip of the spinous process of the ventral (medial) epicondyle of the humerus and from the ventral side of the proximal 6 mm of the *M. flexor digitorum profundus*. Insertion is by an aponeurosis onto the basal and distal thumb pads, on the ventral sesamoids at the first metacarpophalangeal junction, on the anterior face of metacarpal II, about 13 mm distal to its base, and on the ventral aspect of the proximal few millimeters of metacarpals III and V.

The relatively heavy attachments on the first digit and the rather large belly of the palmaris longus in *Desmodus* suggest that this muscle is important in ventral flexion of the thumb during the jump and perhaps in terrestrial locomotion. The attachments on the second and third metacarpals are suited to flex them toward the radius and probably aid the *M. flexor carpi radialis*, *M. flexor carpi ulnaris*, and *M. extensor carpi ulnaris* in keeping the wing tightly folded during the jump and in terrestrial locomotion. When the hand is fully extended in flight, the radial extensors of the hand easily overpower this muscle, but it can function to ventrally brace the second and third metacarpals against the force of the air stream and help strengthen the leading edge of the wing. The attachment to the fifth metacarpal probably serves a relatively passive bracing function, as it is not suited to flex the metacarpal toward the radius.

The electromyographic data for the palmaris longus are not ideal, because the bat did not fully extend the left wing during most of the flight. However, the recorded activity of the muscle is probably similar to that in normal locomotor activity. Sporadic contraction occurs during the step and partial hop before the bat jumps into flight (Fig. 41A–G) and during the powered phase of the jump (Fig. 41H–I). The flick phase does not seem typical (par-

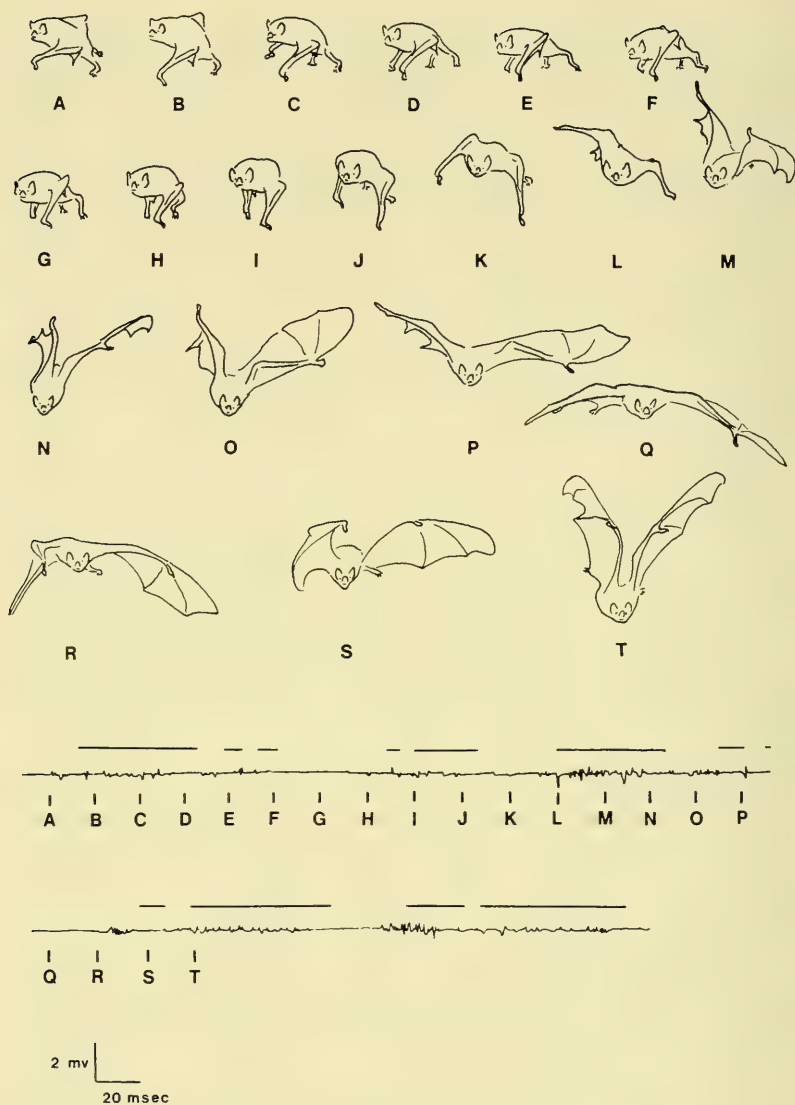


FIG. 41. Electromyogram of right *M. palmaris longus* of *Desmodus* and corresponding locomotor behavior. The contraction of the muscle occurs slightly after the electrical event and is shown as a solid line above the electromyographic recording. Corresponding locomotor stages and portions of the electromyogram are indicated by the same letters.

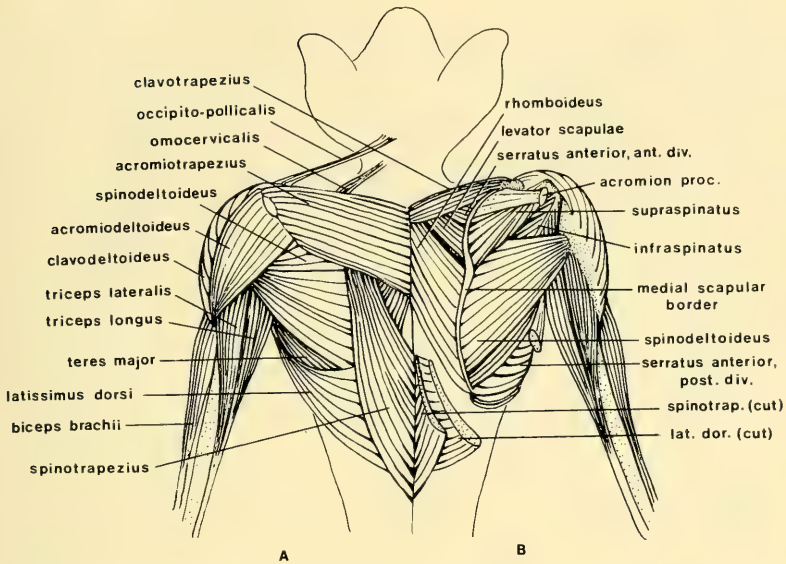


FIG. 42. Dorsal view of pectoral girdle musculature of *Desmodus*. Superficial muscles (left of midline) and view with *M. acromiotrapezius*, *M. spinotrapezius*, *M. latissimus dorsi*, and *M. acromiodeltoideus* removed (right of midline).

ticularly the movements of the right wing with the implanted electrodes), but contraction occurs through this phase, perhaps to “favor” the wing and keep it partially flexed (Fig. 41L–N). Contraction again occurs in the first half of the downstroke and ceases until the middle of the upstroke, when a short burst occurs, perhaps to partially flex the digits and “cock” them for extension in the flick phase (Fig. 41O–S). The contraction at the beginning of the flick phase may be to resist the radial extensors and let their contraction build up maximal tension before relaxation of the palmaris, and perhaps other flexors, suddenly releases the hand. This could contribute to a “snap” of the chiropatagium to provide considerable thrust. The wing is more extended at this point and contraction occurs during the entire downstroke.

M. flexor carpi radialis (Figs. 47, 49).—Origin is on the postero-ventral aspect of the proximal half of the belly of the *M. pronator teres*. Insertion is on a large tubercle on the anteroventral base of metacarpal II.

In phyllostomatids such as *Macrotus*, the insertion of this muscle

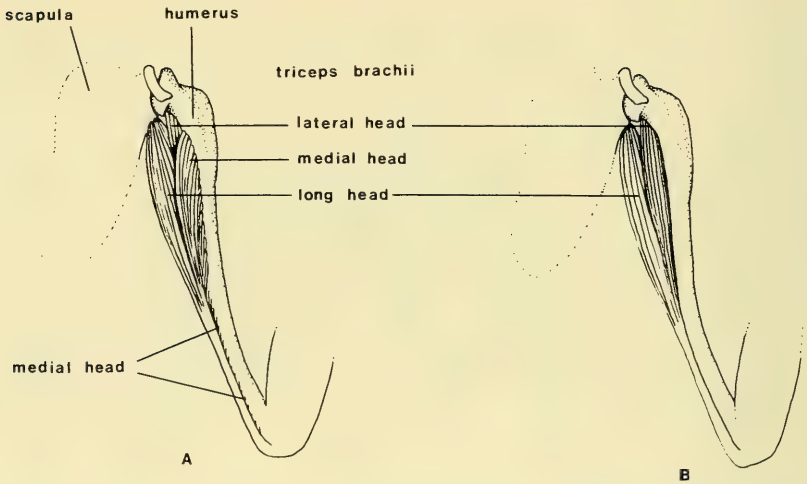


FIG. 43. Ventral view of *M. triceps brachii* of *Desmodus*: A, intact; B, medial head removed.

is on the third metacarpal (Vaughan, 1959). The insertion on metacarpal II in *Desmodus* permits the leading edge of the wing to be actively flexed against the radius rather than passively flexed by flexors of the third, fourth, or fifth digits. The position of the insertion also reflects the need to rapidly fold the wing in an alighting maneuver and to hold it firmly folded during terrestrial locomotion, climbing, and jumping.

M. pronator teres (Fig. 47).—Origin is on the tip of the spinous process of the ventral (medial) epicondyle of the humerus. Insertion is on 10 mm of the ventral aspect of the radius beginning 8 mm distal to the tip of the spinous process.

As the humero-radial articulation allows little but flexion and extension, this muscle acts as a weak flexor and a powerful ventral brace of the radius. In terrestrial locomotion or alighting maneuvers, forces against the carpus are transferred to the humerus as a strong supinating torque. The elbow must be strongly braced against these forces without excessive connective tissue binding that would reduce mobility. Co-contraction of the *M. supinator* also stabilizes the radius against the humerus.

M. flexor digitorum profundus (Figs. 47, 49).—The origin includes the ulna from 5 mm of its interosseus and ventral surface distal to

its contact with the radius; the tip of the spinous process of the humerus; and a few fibers from the posterior surface of the radius 5 mm distal to the spinous process of the humerus. Insertion is as follows: the tendon divides at the carpus into 1) a heavy tendon that inserts on the middle of the ventral aspect of the first phalanx of digit I (a tiny tendon diverges from this tendon and is the origin for a small muscle inserting on the anterolateral aspect of the distal tip of metacarpal I); 2) a tendon that runs over the pisiform and inserts on the proximoventral tips of the first and second phalanges of digit III; and 3) a tendon of origin for one belly on the *M. interossei* that inserts on the posterior surface of metacarpal III, 10 mm distal to its proximal base.

This rather massive muscle supplies most of the ventral flexive force to the thumb as it provides the last upward thrust in the powered phase of the jump. The attachments to the metacarpal and the two proximal phalanges of digit III flex the third digit and help keep the wing tightly folded during the jump and in terrestrial locomotion. Also, all of the forearm flexors of the thumb, the *M. flexor digitorum profundus*, *M. palmaris longus*, and the *M. abductor pollicis longus* have flexive attachments to at least one of the other digits and help keep the chiropatagium folded against the radius during ventral flexion of the thumb.

In flight, contraction of the flexor digitorum profundus would ventrally brace the metacarpal and phalanges of the third digit and could control depression of much of the leading edge of the wing and the degree of upward deflection of the phalanges of digit III by opposing the upward force of the air.

Extensors of the Manus

M. interosseus dorsale (Figs. 48–49).—Origin is on the posteroventral surface of the base of metacarpal II. Insertion is by an aponeurosis on the anteroventral aspect of the tip of metacarpal III and on the proximal half of the anteroventral surface of the first phalanx of digit III.

It seems odd that this muscle should be absent in *Macrotus* and *Myotis* (Vaughan, 1959) and present in *Eumops* (Vaughan, 1959), *Plecotus auritus* (Norberg, 1970*b*), and *Desmodus*. In *Desmodus* it pulls the first phalanx of digit III anteroventrad and tightens the chiropatagium between digits III and IV. It also braces the first

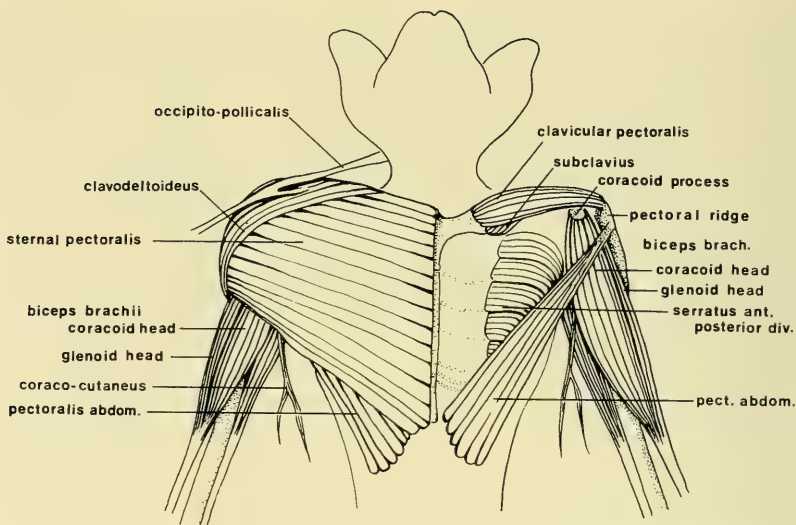


FIG. 44. Ventral view of pectoral girdle musculature of *Desmodus*. Superficial muscles (left of midline) and view with *M. pectoralis*, sternal division, and *M. clavodeltoideus* removed (right of midline).

phalanx of digit III against upward deflection, and limits upward deflection to phalanges two and three.

Flexor Group of the Manus

M. abductor pollicis brevis (Fig. 49).—See the account of *M. abductor pollicis longus*.

M. flexor pollicis brevis (Fig. 49).—Origin is by a long tendon from the anteroventral tip of the lunar and from the ligament between the anterolateral tip of the trapezium and the anterior base of metacarpal II. Insertion is on the medial aspect of the distal tip of metacarpal I and on the lateral aspect of the distal tip of metacarpal I.

The two bellies of this muscle are ventral flexors of metacarpal I if contracting simultaneously and, if contracting singly, are ventrolateral or ventromedial flexors of the first metacarpal. As powerful ventral flexion of the thumb is the function of the *M. flexor digitorum profundus*, *M. palmaris longus*, and *M. abductor pollicis longus*, the flexor pollicis brevis probably is more important in moving

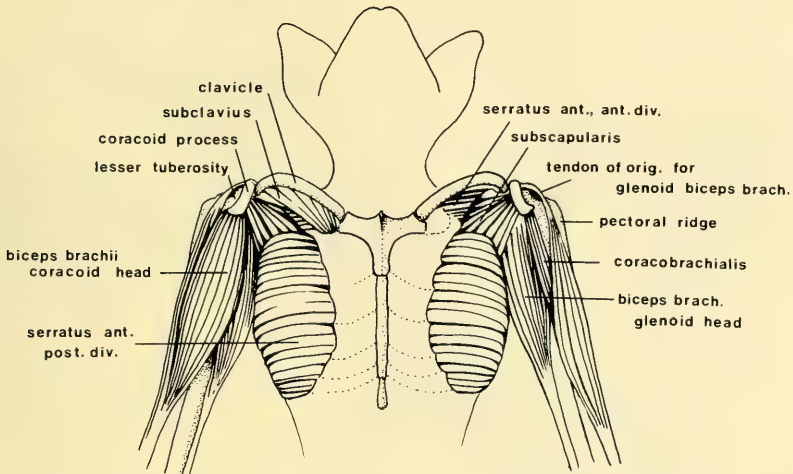


FIG. 45. Ventral view of deep pectoral girdle musculature of *Desmodus*. View (left side) with *M. pectoralis*, sternal division, *M. clavodeltoideus*, *M. pectoralis abdominalis*, *M. pectoralis*, clavicular division, removed and view (right side) with the above-mentioned muscles and the *M. subclavius* and *M. biceps brachii*, coracoid head, removed.

the thumb in delicate maneuvers during terrestrial locomotion or climbing. In elevated walking or in a terrestrial feeding posture, this muscle helps shift the weight from the basal pad of the thumb to the distal pad at the metacarpophalangeal junction (Fig. 2C). When the bat feeds from the neck or head of an animal, the thumbs must be moved occasionally to give the claws purchase on the skin or hair, and these muscles probably function in such movements.

M. adductor pollicis (Figs. 48–49).—Origin is on the anteroventral aspect of metacarpal II, 1.5 mm distal to the insertion of the *M. flexor carpi radialis* and on the ventral aspect of metacarpal III distal to its articulation with the carpus. Insertion is by an aponeurosis on the dorsolateral aspect of the distal tip of metacarpal I and by a tendon on the dorsal base of the second phalanx of digit I.

The more delicate ventrolateral movements of the thumb during terrestrial locomotion, climbing, and perhaps feeding are powered by this muscle and the lateral belly of the *M. flexor pollicis brevis*. If the first metacarpal is braced by both bellies of the latter muscle,

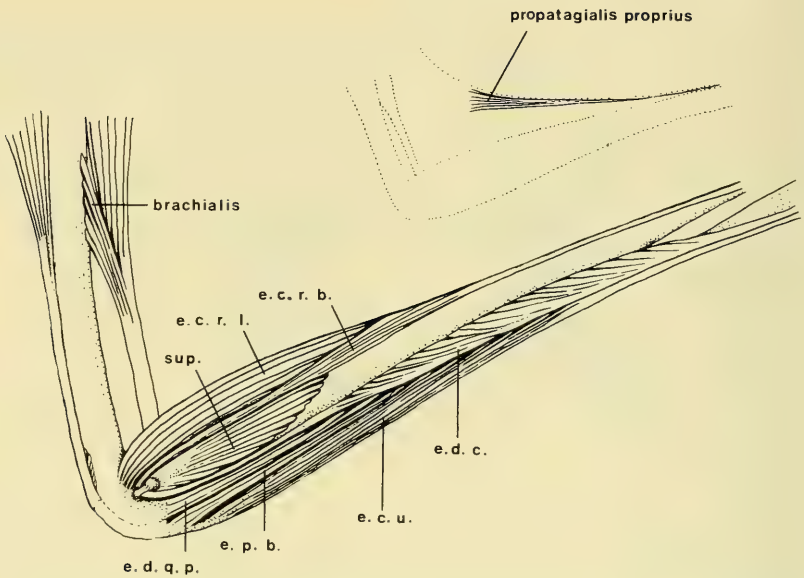


FIG. 46. Dorsal view of superficial musculature of the right forearm of *Desmodus*. Abbreviations: e.c.r.b., *M. extensor carpi radialis brevis*; e.c.r.l., *M. extensor carpi radialis longus*; sup., *M. supinator*; e.d.c., *M. extensor digitorum communis*; e.c.u., *M. extensor carpi ulnaris*; e.p.b., *M. extensor pollicis brevis*; e.d.q.p., *M. extensor digiti quinti proprius*.

the *M. adductor pollicis* could elevate the terminal digit and claw, and draw the entire digit ventrolaterad.

M. interossei (Fig. 49).—Individual muscles of this group are as follows:

1) Origin is by a tendon on the ventral tip of the trapezium. Insertion is on the posterior half of the ventral base of phalanx one, digit III.

Along with the *M. interosseus dorsale*, this muscle stabilizes the first phalanx of digit III against deflection upward by the force of the air stream during adduction of the wing.

2) Origin is from the magnum and a tendon from the ventrolateral aspect of the base of metacarpal IV. Insertion is on the ventrolateral aspect of the tip of metacarpal IV and on the ventrolateral aspect of the proximal tip of phalanx one.

This is a weak flexor of the first phalanx of digit IV and serves, along with the third belly of this group of muscles, to brace the

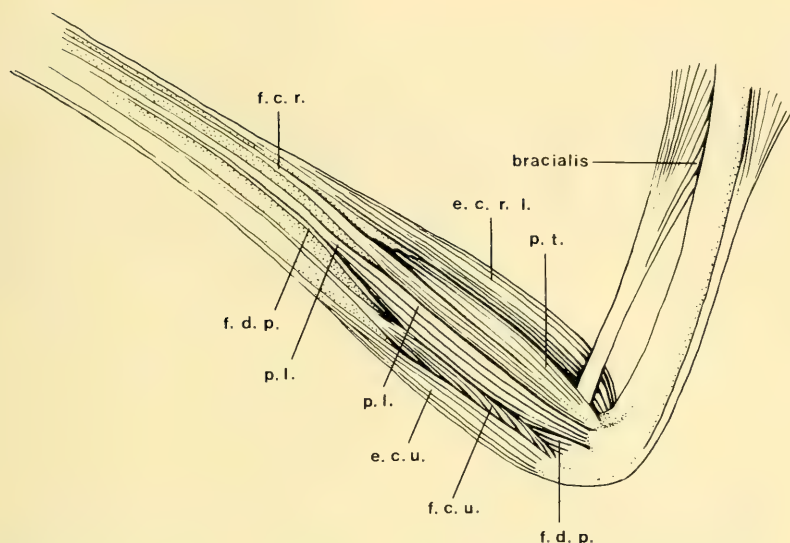


FIG. 47. Ventral view of superficial musculature of the right forearm of *Desmodus*. Abbreviations: f.c.r., *M. flexor carpi radialis*; e.c.r.l., *M. extensor carpi radialis longus*; p.t., *M. pronator teres*; f.d.p., *M. flexor digitorum profundus*; p.l., *M. palmaris longus*; e.c.u., *M. extensor carpi ulnaris*; f.c.u., *M. flexor carpi ulnaris*.

fourth metacarpal against upward deflection during adduction of the wing. It also assists in flexing the phalanges as the wing is folded during an alighting maneuver or for terrestrial locomotion.

3) Origin is from the magnum and a small tendon from the ventromedial aspect of the proximal base of metacarpal IV. Insertion is on the ventral base of the first phalanx of digit IV by a tendon.

This muscle works along with the second belly of this group, and its function is essentially identical.

4) Origin is from a slip of the tendon of the *M. flexor digitorum profundus*. Insertion is on the posteromedial surface of metacarpal III 10 mm distad to its proximal tip.

When the *M. flexor digitorum profundus* contracts to ventrally flex the thumb during a jump or in terrestrial locomotion, the origin of this muscle is stretched, and the force, transmitted through the belly, flexes the third digit against the radius. Contraction of this belly of the *M. interosseus* under these conditions applies more force

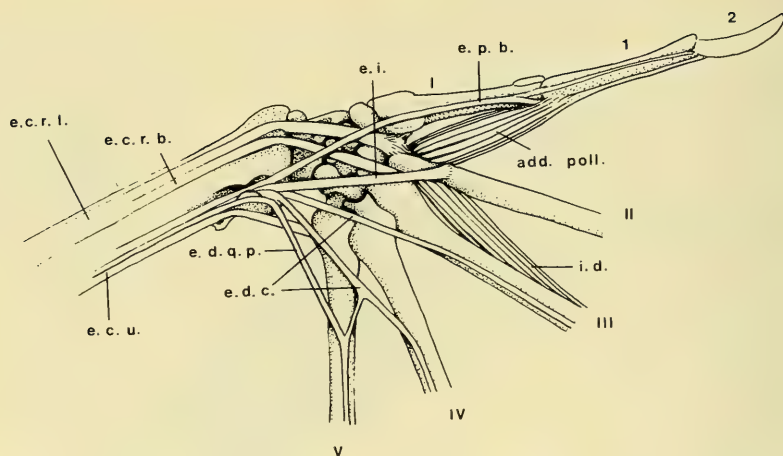


FIG. 48. Dorsal view of the musculature and tendons of the right carpus of *Desmodus*. All of the *M. extensor indicis*, except its major insertional tendon, is removed. Abbreviations: e.c.r.l., *M. extensor carpi radialis longus*; e.c.r.b., *M. extensor carpi radialis brevis*; e.i., *M. extensor indicis* (major tendon); e.p.b., *M. extensor pollicis brevis*; e.c.u., *M. extensor carpi ulnaris*; e.d.q.p., *M. extensor digiti quinti proprius*; e.d.c., *M. extensor digitorum communis*; i.d., *M. interosseus dorsale*; add. poll., *M. adductor pollicis*; I-V, metacarpals I-V; 1, 2, phalanges of digit I.

and holds the third digit against the radius more firmly. When the wing is extended during the wingbeat cycle, the elastic properties of this muscle allow contraction of the *M. flexor digitorum profundus* to ventrally brace the third metacarpal and first phalanx of digit III but only apply minimal flexive force.

M. abductor digiti quinti (Fig. 49).—Origin is by a tendon from the posterior tip of the scaphoid. Insertion is by a broad aponeurosis on the ventromedial aspect of the distal tip of metacarpal V and on the ventromedial base of phalanx one.

This muscle is large in *Desmodus* and is situated to brace the fifth metacarpal against the force of the airstream during adduction of the wing and ventrally flex the first phalanx of digit V. In *Macrotus* (Vaughan, 1959), this muscle is quite tendinous and acts as an inelastic brace; however, the relatively large, fleshy belly suggests its function is more variable in *Desmodus*. Relaxation during the first half of the downstroke allows the upward deflection of the phalanges (Fig. 19), which provides thrust from the middle of the wing. Contraction ventrally flexes the phalanges and shapes this

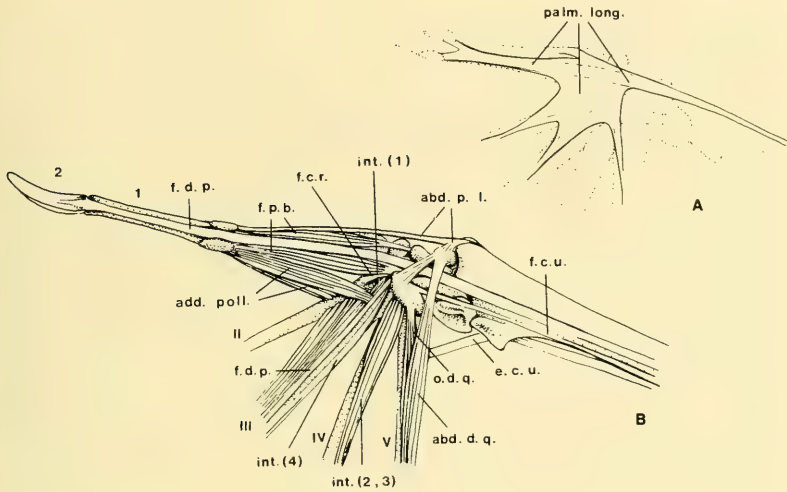


FIG. 49. Ventral view of the musculature and tendons of the right carpus of *Desmodus*: A, view of the insertion of the *M. palmaris longus*; B, view of the anatomy with the palmaris removed. Abbreviations: f.c.u., *M. flexor carpi ulnaris*; abd. p.l., *M. abductor pollicis longus* (and perhaps *brevis*); int. (1–4), bellies of *Mm. interossei*; f.c.r., *M. flexor carpi radialis*; f.p.b., *M. flexor pollicis brevis*; f.d.p., *M. flexor digitorum profundus*; add. poll., *M. adductor pollicis*; abd. d.q., *M. abductor digiti quinti*; o.d.q., *M. opponens digiti quinti*; e.c.u., *M. extensor carpi ulnaris*; II–V, metacarpals of digits II–V (metacarpal I not visible); 1, 2, phalanges of digit I.

part of the wing into a cambered surface suited for production of lift. This function is probably aided by contraction of the *M. abductor pollicis longus*, which displaces the origin proximally.

M. opponens digiti quinti (Fig. 49).—Origin is by a tendon on a tubercle of the posteroventral aspect of the pisiform adjacent to its articulation with metacarpal V. Insertion is by an aponeurosis on the ventrolateral aspect of the tip of metacarpal V.

The tendons of this muscle and the *M. abductor digiti quinti* fuse distally, thus their function is essentially the same. However, because the opponens digiti quinti originates on the pisiform, it is not affected by contraction of the *M. abductor pollicis longus* and can flex the phalanges of the fifth digit, even if the abductor is relaxed. Co-contraction of all three can powerfully flex the phalanges and overpower the *M. extensor digiti quinti proprius* to hold the fifth digit at a high and rigid camber.

DISCUSSION

Terrestrial Locomotor Behavior

Desmodus rotundus is the most terrestrially oriented of bats; its agility in quadrupedal locomotion far surpasses that of other species and even that of many small rodents and carnivores. As several authors have described (Beebe, 1927; Price, 1950; Ditmars and Greenhall, 1935, 1936; Dalquest, 1955; Wimsatt, 1959), it runs along horizontal or vertical surfaces with ease and executes sudden evasive maneuvers that make it difficult to capture. This terrestrial facility is closely involved with feeding behavior, as no other bat except *Desmodus* (and perhaps the other sanguivorous bats, *Diaemus* and *Diphylla*) shows such agility in terrestrial locomotion. Observations of *Desmodus* scrambling over the backs and necks of host animals prior to feeding (or to avoid movements of the host animal to brush them off), and running or hopping about on the ground while feeding, illustrate the adaptive value of this effective terrestrial locomotion. Although several other species of bats easily move about on the ground and occasionally catch food to alight prior to catching the food, *Desmodus*, and perhaps to a lesser extent the other two sanguivorous bats, are the only chiropterans that have become so specialized in feeding as quadrupeds.

According to Vaughan (1959, 1970*d*, 1970*e*), bats probably evolved as crevice dwellers and thus, initially, were adapted for terrestrial locomotion in confined spaces. Even in bats such as *Eumops perotis*, *Myotis velifer* (Vaughan, 1959), *Antrozous pallidus* (Burt, 1934), *Nyctalus noctula* (Anonymous, 1969), *Rhinolophus ferrumequinum* (Southern, 1964), and *Eptesicus fuscus* (Altenbach, 1968), which readily move about in quadrupedal fashion on the ground or other surfaces, the limbs are directed more or less lateral to the body, which is typically held quite close to the surface. The power strokes are directed posterolaterally by flexion and slight pronation of the brachii, extension of the elbows, and by posterior swings of the laterally extended pelvic limbs. These types of movements are necessary in a crevice or in confined roosts, but are inefficient, inasmuch as the weight is supported on laterally directed limbs. The large *M. pectoralis* is well suited to support much of the weight,

but the muscles that move the limbs have to work against the forces that maintain posture.

As described in the section on locomotion, *Desmodus* inclines the body and holds it well above a horizontal surface when walking or running. The shanks are directed almost vertically, the brachii are directed relatively posterolaterally, and the forearms are partially flexed and directed anteroventrally and slightly laterally. The net result of this posture is that the contact of the limbs with the surface is shifted nearer the body and more below it, requiring less effort to maintain the posture. Thus greater muscular effort can be devoted to moving the limbs, resulting in more rapid and complex movements. Posteroventral thrusts with both pectoral and pelvic limbs produce a hopping gait that rapidly carries the bat over the ground and allows chasing of host animals.

The orientation of the hind limbs makes them well suited to pulling, thus the bats typically climb backwards. The pectoral limbs incline the body away from the surface and aid climbing by forward thrusts. With the body in a climbing position, the pectoral limbs are able to thrust the bat outward into flight or laterally in an avoidance reaction. There are few records of predators feeding upon bats in roosts, thus the agility on vertical surfaces in roosts appears to be a secondary advantage of locomotor mechanisms evolved for terrestrial feeding.

Desmodus regularly consumes a large volume of blood, often as much as 100 per cent of its body weight, in a single feeding period (Wimsatt, 1969). This, and the habit of feeding from the ground or moving about on the ground between feeding periods, require the ability to launch into flight from the ground when heavily loaded. Host species, such as large ungulates, often are found in the open and some distance from trees or rock outcrops on which the bats could climb and from which they could drop into flight. Many other species of bats require a drop from a roost to build the air speed necessary for flight. Bats other than *Desmodus* that can fly from the ground, such as some nectar feeding species (*Leptonycteris*, *Glossophaga*) and lightly-loaded insectivorous taxa (*Antrozous*, *Myotis*, *Plecotus*), push off from the surface with partially or fully extended wings and begin flight with a lift-generating wing-beat cycle.

The ability to shift the pectoral limbs almost directly under the

body and several other anatomical modifications allow *Desmodus* to achieve flight from the ground by a powerful jump, which carries it, even when fully gorged on blood, high enough above the surface to initiate a high-amplitude wingbeat cycle. The jump is effected by a powerful adduction of the brachii, extension of the elbows, and ventral flexion of the thumbs. The extreme elongation of the thumbs, which are proportionally longer than in any other bat, provides a long lever arm for this flexive movement that adds the final upward momentum during the jump. The pelvic limbs supply little of the upward thrust, as they function primarily to shift the center of gravity over the powerful pectoral limbs. The jumping behavior also plays an important role in avoiding being stepped on by a large host animal and perhaps avoiding terrestrial predators. Although jumps into flight are directed primarily forward and upward, a direction that allows maximal thrust from the pectoral limbs, avoidance jumps can occur in any direction. Both avoidance jumps and jumps into flight are powered by the pectoral limbs, while the hind limbs shift the weight into the line of the jump.

Alighting maneuvers on a horizontal surface are essentially the reverse of the movements used in a jump into flight. Contact with the substrate is made first with the thumbs. The downward momentum is slowed by muscular resistance to hyperextension of the thumbs, flexion of the elbows, and abduction of the brachii. The movement effectively breaks the force of the landing and is probably advantageous for alighting softly on or near a host animal. Rodney Honeycutt, Ira Greenbaum, and Robert Baker (personal communication) speculate that because obligate blood feeding appears in mammals only in the genera *Desmodus*, *Diphylla*, and *Diaemus*, these bats probably evolved from a common ancestor that was already a sanguivore. I cannot speculate about the evolutionary development of sanguivory in bats, but I feel that *Desmodus* is certainly the most derived, from a locomotor morphological standpoint, of the Desmodontinae. The morphological modifications of the limbs and girdles reflect selective pressures somewhat different than those expected to have acted on a bat that typically parasitizes large domestic animals of man.

The habit of feeding on large ungulates from the ground, and the ability to feed from relatively active terrestrial rodents, suggest that perhaps the bats initially fed on small terrestrial mammals or other vertebrates and that the facility for terrestrial locomotion

developed in response to this mode of feeding. Seemingly, if the bats had fed initially on large ungulates, they could have readily fed from the back or neck and the ability to run on the ground would not have been necessary. With only a small thrust of the limbs, the bats could have dropped off the back or neck into flight. Thus, the complex energy-demanding jump would not have been necessary. Probably the mechanisms of the jump evolved as a means to rapidly negotiate rough terrain in pursuit of a small mammal or other vertebrate, rather than to avoid movements of larger animals. Elongation of the thumbs, no doubt, facilitated rapid locomotion and permitted increasingly longer hops. Transition from a long hop to flight by initiation of the wingbeat cycle does not seem a great step. Once developed, the jumping behavior probably allowed larger meals to be taken in a single feeding period and perhaps permitted feeding on the limbs of larger animals, as it facilitated avoidance maneuvers.

Flight and Aerodynamic Considerations

Investigators of bat locomotor morphology have characterized bats as relatively derived or underderived on the basis of the degree of anatomical and behavioral modification contributing to efficient flight. In most species characterized by efficient flight, sometimes described as relatively derived, there are anatomical features of the pectoral limbs and girdles that automatically move distal parts of the wings when more medial parts are moved. These features also limit the planes of movement possible for the wings, but permit great mechanical advantage for muscles to power the movements and allow concentration of muscle mass nearer the center of gravity. Such species can fly rapidly over relatively long distances with minimal energy expenditure and are well suited for long feeding periods in flight or for migration.

Species with inefficient flight, often characterized as underderived, are better suited to feeding on nectar or fruits, or feeding and maneuvering in a cluttered environment, and necessarily lack the anatomical features that restrict planes of movement and provide automatic movements of more distal parts of the wings. The greater variability of movements permits slow, intricate, or hovering flight or terrestrial locomotion necessary for feeding.

It is important to note that the morphological features of the

limb and girdle that permit either highly efficient flight (or flexible, relatively inefficient flight) may be equally derived and probably reflect considerable evolutionary modification. *Desmodus* is certainly an example of a morphologically derived bat that has specialized in the tremendous variability and amplitude of movements that are necessary for flight, rapid terrestrial locomotion, and also for jumping, which effects the transition between flight and terrestrial locomotion.

The momentum imparted by the jump is sufficient to carry the body approximately 20 to 30 cm above the ground, giving the bat time to unfold and position the wings for the first downstroke. However, both forward and upward velocity rapidly decrease during this coasting phase. *Desmodus* derives forward thrust from unfolding the wings, which is similar to a movement in the last half of the upstroke in *Desmodus* and in certain other phyllostomatid (Altenbach, 1968), vespertilionid, and rhinolophid bats (Eisentraut, 1936), and which Norberg (1970a) termed the flick phase. In this movement the digits and forearm are extended and the entire arm is powerfully abducted and pronated. The dorsal surface of the wing is directed posteriorly and dorsally against the air stream, thus providing a component of forward thrust to reinforce the forward momentum of the bat prior to initiation of the wingbeat cycle. Several muscles power this flick; thus it can generate more thrust than can abduction of the wing alone.

The wingbeat cycle of *Desmodus* is peculiar because it shows both the high amplitude downstroke typical of many vespertilionid bats and the extended wing, low drag upstroke, and flick typical of the phyllostomatid nectar-feeders to which *Desmodus* is closely related (Forman *et al.*, 1968). The same morphological features of the shoulder girdle that permit the limbs to be directed ventral to the body in terrestrial locomotion and in the jump allow a downstroke of high amplitude. Although the flick, prior to the first downstroke after a jump, supplies some increase in forward speed, the air speed and upward velocity are low at the start of the downstroke; thus maximal thrust and lift are necessary to initiate forward flight. As in other bats (Eisentraut, 1936; Vaughan, 1959, 1970d; Altenbach, 1968; Norberg, 1970a), the force of the air as the wing is adducted deflects the phalanges of digit IV upward, thus making the portion of the wing adjacent to digit IV a thrusting surface. However, the arm is strongly pronated to orient the leading edge

of the wing well below the trailing edge, forming all but the proximal third of the plagiopatagium and the chiropatagium, nearly 80 per cent of the wing area, into a thrusting structure. This contrasts sharply with published estimates that only 20 per cent of the wing area is configured to provide thrust in other bats. Photographs taken several wingbeats after initiation of flight indicate that the phalanges of the fifth digit also are deflected upward to increase this thrusting effect. The distal portion of the chiropatagium often is not fully unfolded during the first, and occasionally the second or third, downstroke; yet motion pictures indicate rapid acceleration during this period. Obviously, thrust is being produced by the more medial parts of the wing and not by just the propeller effect of the distal chiropatagium as is typically described for bat flight. During the downstroke, both the upward and forward velocity of the body increases, apparently the result of downward and backward acceleration of air produced by the adduction of the wings. Eisentraut (1936) stated that upward drive is produced by the adduction of the wings in the downstroke but more recent discussions of bat flight (Vaughan, 1959, 1966, 1970*d*, 1970*e*) suggest lift is only produced by air flow over a cambered surface. In *Desmodus*, as in any bat, the latter is perhaps the case in more rapid forward flight. However, at least in *Desmodus*, much of the lift in the initial flight following a jump and in the slow accelerating flight that follows, is the result of acceleration of air ventrally during adduction of the wings.

An upward deflection of the distal two phalanges of digit III during the downstroke perhaps reduces the formation of tip vortices and, during the last half of the stroke, provides additional lift. Adduction of the wings continues slightly anteriorly in the last half of the downstroke and the tips occasionally meet below the body. The high amplitude of the stroke permits production of continuous air acceleration and thus thrust and lift production for a relatively long period.

As in some nectar-feeding species of phyllostomatids, the downstroke gives way to the upstroke by a gradual change of direction and position of the wing. Drag is minimized by raising the wings anterior to the body, while they are fully extended, and with the plane oriented vertically. A pronounced flick, similar to that described by Eisentraut (1936) and Norberg (1970*a*) in other species, completes the upstroke and provides additional thrust. The flick

can occur only in bats with great freedom of movement of the arm and hand. In species that have evolved more efficient, high-speed flight, anatomical modifications of the pectoral limb allow more automatic extension and flexion of the hand and centralization of weight and do not permit this type of upstroke and flick. There is little doubt that this movement produces forward thrust in *Desmodus*, as Eisentraut (1936) believed it does in several other species. The most conclusive evidence is the rapid acceleration during this movement prior to the first upstroke following a jump. Although of greater amplitude, the initial flick is similar to that observed in subsequent wingbeats of slow forward flight. There is only slight flexion of the digits toward the forearm during the first half of the upstroke in slow forward flight, thus extension of the digits plays a lesser role in flight than it does in the initial flick.

Although no high-speed photographic data are available on rapid flight, the flick is certainly more important in slow flight than in rapid flight. During the flick, thrust is derived by a posterior swing of the more distal portions of the wing against the air. Obviously, as the forward speed of the bat increases, the thrust from the flick decreases. The high thrust required during the initial flight following a jump is probably not so vital at high cruising speeds and the upstroke is basically a recovery stroke. There is almost certainly a modification of the wingbeat cycle during rapid forward flight, but it remains for high-speed photographs to illustrate it. Perhaps the amplitude of the downstroke is less and the stroke begins at a lower angle above horizontal (and continues quite deep), as in some molossid bats, which are best suited for this type of flight (Vaughan, 1959, 1966, 1970d). Inasmuch as *Desmodus* is anatomically suited for the upstroke with the wing positioned anterior to the body and its plane oriented vertically, this portion of the stroke may remain relatively unchanged, and a pronounced flick may occur. However, it may be more passive than in initial flight after a jump or in slow forward flight.

Desmodus has a heavy wing loading ($4.8 \text{ cm}^2/\text{g}$), as do molossids such as *Molossus bondae* ($4.0 \text{ cm}^2/\text{g}$), and phyllostomatids such as *Phyllostomus hastatus* ($3.4 \text{ cm}^2/\text{g}$), and *Artibeus jamaicensis* ($4.5 \text{ cm}^2/\text{g}$)—Hartman, (1963). However, its aspect ratio is low (2.66) as compared to *Molossus bondae* (3.6) and *Phyllostomus hastatus* (3.48). Struhsaker's data (1966), calculated by slightly different methods, place *Desmodus* (4.9) and *Leptonycteris sanborni* (4.6) below *Molossus*

nigricans (5.9) and *Tadarida brasiliensis* (6.7), and above several species varying from 4.13 (*Myotis velifer*) to 2.44 (*Antrozous pallidus*).

These data illustrate that *Desmodus* is somewhat unique in having both a heavy wing loading and a low aspect ratio. Other investigators have associated high aspect ratio and high wing loading with relatively high-speed, unmaneuverable direct flight, such as that of many molossid bats. Many of the species with low aspect ratio wings, such as *Antrozous pallidus*, *Myotis lucifugus*, and *Pipistrellus hesperus* are lightly loaded and have delicate, even hovering, flight. Although *Leptonycteris* is less heavily loaded than is *Desmodus*, Struhsaker (1961) found its loading more comparable to *Desmodus* than to the other bats he investigated. The flight of these two bats, however, is quite different. In slow and hovering flight, *Leptonycteris* gains high lift from a medial and anterior swing of the forearm and hand produced by a flexion of the elbow in the last half of the downstroke (Altenbach, 1968). This movement supplies lift without movement of the body through the air stream. The length of the hand compared to that of the arm is relatively greater in *Leptonycteris* than in *Desmodus* (Findley *et al.*, 1972) and reflects the role of the hand in lift production. *Desmodus* exhibits no such modification of the wingbeat cycle, and the relatively shorter and smaller hand-wing probably reflects evolutionary compromises for both flight and terrestrial locomotion. *Desmodus* appears to utilize a high amplitude downstroke to provide maximal thrust and lift during the wingbeat cycles following a jump. As thrust is certainly produced during the downstroke by much of the plagiopatagium in addition to the chiropatagium, a large chiropatagium is not necessary for thrust production. Elongation of the wings would be disadvantageous, because the jump carries the bat less than 0.3 m above the ground and contact of the wings with the ground at the bottom of a deep stroke would certainly reduce acceleration. The short hand can be folded quickly in an alighting maneuver to prevent damage to the rather delicate digits and, when folded, is not bulky enough to hamper quick movements necessary in the rapid terrestrial locomotion typical of this bat.

The need for a relatively long limb in quadrupedal locomotion and particularly for jumping probably prevents reduction in the length of the antebrachium and brachium. Thus, to maintain a wing of the proportions necessary for production of high thrust and lift, and, at the same time to keep its length minimal and

provide a long limb for quadrupedal locomotion and jumping, the relative length of the hand is reduced.

Since flight serves primarily to move the vampire bat relatively short distances between roosting and feeding areas, there is no need of anatomical modification for highly efficient flight, typical of species that feed in flight or cover long distances in feeding and migration. Great freedom of movement of the limbs, however, is necessary in the terrestrial feeding behavior of this bat and especially for the transition from terrestrial locomotion to flight. Thus specialization of the appendicular anatomy has been toward extreme variability and amplitude as well as independence of movement. Features that allow maximal muscular mass to power high energy demanding movements have permitted development of jumping behavior for transition between terrestrial and aerial modes of locomotion. Some of these same features also permit extremely high thrust and lift production necessary to sustain flight after a jump and while carrying a heavy load of blood.

In effect, *Desmodus* has specialized in variability to feed as a terrestrial vertebrate and yet retain the advantages of a flying vertebrate. Thus, this bat has reduced competition with other bats for food resources, yet has retained the advantage of mobility and ability to use secluded roosts that are inaccessible to most predators.

Anatomical Considerations

Perhaps the most striking osteological feature of the pectoral girdle is the nature of articulation of the clavicle and scapula, which allows the scapula to rock freely about its long axis. In other species of bats such as *Plecotus auritus* (Norberg, 1970b), *Eumops perotis* and *Myotis velifer* (Vaughan, 1959), and *Eptesicus fuscus* (Altenbach, 1968), the clavicle is bound distally to both the acromion process and the base of the coracoid process. This feature stabilizes the pectoral girdle and gives the muscles that rock the scapula and the wing, when the humerus and scapula are locked dorsally or ventrally, great mechanical advantage. However, the amplitude and variability of movements of the wing are greatly restricted. Thus, efficiency is gained at the expense of flexibility of movement. In phyllostomatids such as *Leptonycteris sanborni* (Altenbach, 1968) and *Macrotus waterhousii* (Vaughan, 1959), the articulation of the scap-

ula and clavicle is similar to that of *Desmodus*, but the arrangement in *Desmodus* allows much greater freedom of movement.

The relatively small angle through which the humerus can be adducted or abducted relative to the scapula is surprising, considering the great amplitude of the movement of the brachium during terrestrial locomotion, jumping, and flight, but suggests that some of the muscles that insert on the scapula (*M. serratus anterior*, trapezius group, and *M. rhomboideus*) are important in moving the arm. The spinous process of the ventral (median) epicondyle of the humerus has no distal projection typical of many fast-flying molossid, vespertilionid, and mormoopid bats; thus, muscles originating from it are not affected by movements at the elbow.

The ulna is strongly fused to the radius distally and rigidly articulated with it proximally. The elevated carriage of the body in terrestrial locomotion and jumping in this bat directs forces against the long axis of the forearm, thus bracing is needed. In addition, the relative independence of the hand from movement at the elbow requires more muscle mass in the forearm, and the rigid ulna supplies a solid structure for the origin of such muscle. Investment of the distal end of the radius with deep grooves and ridges for confinement of insertional tendons of forearm muscles reflects the large forces involved during terrestrial locomotion and jumping.

The carpus is not highly specialized except, as in other bats, to limit the movements of all but digit I to a single plane, thus bracing the hand-wing against the forces of the air stream in flight. However, digit I is greatly elongated, almost 30 per cent the length of the forearm, and the articulation of the first metacarpal and trapezium allows considerable freedom of movement. The articulation is bound by ligaments ventrally and the articular surfaces slope away dorsally from the ventral binding, allowing the thumb to be oriented laterally when the forearm is directed perpendicularly against a surface. The thumb thereby functions in maintaining balance when the body is elevated in terrestrial locomotion, and can be flexed powerfully from this position to supply the last upward thrust in a jump and to provide thrust in rapid terrestrial locomotion.

The metacarpophalangeal joints of digits IV and V and the first interphalangeal joint of digit III permit considerable upward deflection of the phalangeal elements distal to them, thus enabling the posterior part of the chiropatagium and distal part of the pla-

giopatagium to supply high thrust during the downstroke. This appears unique among bats as, in others, only the phalanges of digit IV deflect upward to provide the propeller effect described by Vaughan (1959) and Eisentraut (1936).

The myology of the pectoral girdle and limb was described in detail earlier and only the outstanding features, unique to *Desmodus*, will be discussed here.

The *M. clavotrapezius* is large and its complete separation from the *M. acromiotrapezius* and its heavy origin reflect importance in bracing and moving the clavicle. In bats that have the clavicle bound in two points to the scapula, the division between these muscles is obscure and their function nearly identical, inasmuch as rotational forces applied to the scapula are transferred directly to the clavicle. The antagonist of the *M. clavotrapezius*, the *M. subclavius*, also is large, and together these muscles stabilize the clavicle and probably lower and raise it during jumping and flight. The remainder of the trapezius group functions much as in other bats to stabilize the scapula and rock it about its long axis.

Electromyographic data indicate the deltoid group, at least the acromio- and spinodeltoids, functions to stabilize the dorsal scapulohumeral articulation during the powered phase of the jump and much of the downstroke in forward flight. This indicates, indirectly, that the posterior division of the *M. serratus anterior* aids the *M. pectoralis* in adducting the humerus through nearly the entire jump and much of the downstroke. Vaughan (1959) suggested that in other bats, particularly those having the scapula and clavicle bound in two places, the posterior division of the serratus only stops the upstroke and initiates the downstroke, the remainder of the downstroke being powered by the *M. pectoralis* and *M. subscapularis* as they adduct the humerus using the scapula as a fulcrum. In *Desmodus*, the two largest pectoral muscles, the *M. pectoralis* and the posterior division of *M. serratus anterior*, are possibly responsible for nearly all of the brachial adduction in a jump and for much of the brachial adduction in flight.

The *M. clavodeltoideus* is situated to extend the humerus, and its size and complete separation from the clavicular *M. pectoralis* suggest importance of this movement, which produces a power stroke in backward climbing and in positioning the pectoral limbs for alighting on a horizontal surface.

The pronators of the arm, the *M. latissimus dorsi*, *M. pectoralis*

abdominalis, *M. teres major*, *M. subscapularis*, and the posteriormost fibers of the sternal *M. pectoralis* play an important role in the flick phase of the upstroke. Pronation of the arms after initial abduction of the wings in a vertical orientation anterior to the body swings the distal half of the wings posteriorly against the air and provides forward thrust. Although Eisentraut (1936) described the flick and believed it produced thrust in several species of bats, recent investigators have implied the entire upstroke is entirely a recovery stroke and provides no thrust. Indeed, in the molossids and many vespertilionids, particularly those with features that limit freedom of movement of the wings and provide highly efficient flight, the flick is nearly impossible and the upstroke is a recovery stroke. However, in rhinolophids, a few vespertilionids (Eisentraut, 1936; Norberg, 1970a), and many phyllostomatids, including *Desmodus*, the flick is important in providing thrust, as the relatively large size of the muscles involved and the good mechanical advantage for the movements they power, suggest. In addition to the above-mentioned muscles the three heads of the *M. triceps brachii* extend the elbow to aid this movement, and the two largest forearm muscles, the *M. extensor carpi radialis longus* and *M. extensor carpi radialis brevis*, along with the *M. extensor indicis*, powerfully extend the chiropatagium. The relatively small acromio- and spinodeltoids are certainly not large enough to power a thrust-producing upstroke, but they are well suited to raise the wing anteriorly to the body by supination of the humerus and thus elevate the flexed forearm. This type of upstroke seems quite typical of most phyllostomatids, rhinolophids, some vespertilionids, and certainly *Desmodus*. It reduces drag initially and positions the wing for the flick, in contrast to the case in the molossids and mormoopids where the upstroke is a recovery stroke and the entire movement is essentially wasted effort.

The *M. biceps brachii* is adapted to provide a strong, supinating force to the arm and to flex the forearm as in other species. It probably aids somewhat in the downstroke, even though the humerus is dorsally locked with the scapular border. However, its main function is very likely control of rotational stability of the arm and flexion of the forearm at the first of the upstroke.

The importance of the thumb in *Desmodus* is evidenced by the size of the tendons and bellies of the muscles that ventrally flex it. The *M. flexor digitorum profundus*, the *M. palmaris longus*, and the

M. abductor pollicis longus all have large tendons running to the ventral aspect of the first digit. In other bats, the *M. abductor pollicis longus* inserts on the scaphoid, and, in at least one species, *Plecotus auritus*, the *M. abductor pollicis brevis* originates there and inserts on the first digit. In *Desmodus*, the latter muscle has become tendinous and originates directly on the tendon of the former, thus permitting a longer and larger forearm muscle to power the flexion of the thumb. The muscles of the hand, *M. abductor pollicis* and *M. flexor pollicis brevis*, which insert ventrally on the thumb, are well suited to move the thumb to give the claw purchase in such maneuvers as climbing or walking. All of the above-mentioned forearm flexors of the thumb have at least one flexive attachment to digits II through V. Thus, as they flex the thumb in a jump or in terrestrial locomotion, they also aid in keeping the digits flexed toward the forearm and flex the phalanges. The major flexor of the hand wing, the *M. extensor carpi ulnaris*, inserts on the medial base of metacarpal V where it has great mechanical advantage. The insertional tendon is massive and suggests the importance of this muscle in holding digit V and, because of ligamentous attachments between the metacarpals of digits III and V, the rest of the hand-wing against the forearm, and in rapidly folding the hand-wing during an alighting maneuver. The other major flexor of the hand, the *M. flexor carpi ulnaris*, inserts on the pisiform as in other species, but is small and probably only weakly assists *M. extensor carpi ulnaris*. *M. flexor carpi radialis* is best suited to ventrally brace the second metacarpal, and thus the leading edge of the hand-wing. This is important when the leading edge of the wing is oriented below the trailing edge for high thrust production in the downstroke.

Because of the capacity for upward deflection of the phalanges of digits IV and V and all but the basal phalanx of digit III, and the capacity to vary greatly the degree of pronation or supination of the arm, *Desmodus* can vary greatly the angle of attack, camber, and degree of thrusting configuration of the wing. *M. extensor digitorum communis* is well suited to actively deflect the phalanges of digits III and IV, and the *M. extensor digiti quinti proprius* is suited to deflect the phalanges of digit V. The upward deflection of the phalanges of digit V is evident only during about the first half of the downstroke, whereas that of digits III and IV persists to the end of the downstroke. Thus it is critical that there be independent

control of digit V. As *M. abductor digiti quinti* originates on the scaphoid in *Desmodus*, flexion of the phalanges of digit V is partially under control of the *M. abductor pollicis longus*, which inserts on the scaphoid and first digit. Along with the *M. opponens digiti quinti*, these muscles can ventrally flex the phalanges of digit V to eliminate the thrusting contour of the wing in that region and transform it into a more cambered lift-generating surface. During a jump or in terrestrial locomotion, the *M. abductor pollicis longus* can keep the phalanges of the fifth digit flexed as it flexes the thumb by pulling the origin of the *M. abductor digiti quinti*.

The large *M. extensor carpi radialis longus* and *M. extensor carpi radialis brevis* originate medial to the center of the elbow joint and thus are stretched slightly by extension of the elbow. However, they are not invested in a tough connective tissue sheath of deep fascia, as is the case in many molossids and vespertilionids, and do not automatically extend the digits when the elbow is extended. When the flexors of the hand-wing relax, particularly if the elbow is partially or fully extended, these muscles can powerfully and rapidly extend the fingers.

SUMMARY

THE mechanisms of terrestrial locomotion, jumping behavior, and flight of the common vampire bat, *Desmodus rotundus*, were analyzed with high-speed photographs and electromyographs, and were correlated with osteological and myological features of the pectoral girdle and limbs. Great freedom of movement at the articulation of the scapula and clavicle, and independence of movement in the arm and hand, allow the pectoral limbs to be positioned below the body for efficient, rapid, and extremely agile terrestrial locomotion. These same anatomical modifications, coupled with specialization at the shoulder joint, enable the two largest muscles in the bat, the *M. pectoralis* and the posterior division of the *M. serratus anterior*, to power a deep adduction of the arms to effect a jump into flight. Extreme elongation and development of powerful associated flexor musculature permit the thumbs to provide an additional upward thrust in the jump. The jump is vital to achieve flight after taking a blood meal from a prey animal on the ground. The anatomical features of the pectoral girdle and limb

that facilitate both the jump and the remarkable terrestrial locomotion are the most spectacular anatomical modifications in this bat. They suggest *Desmodus* became evolutionarily specialized for feeding terrestrially from small active prey animals. Feeding from the backs or necks of large prey species seemingly would not have necessitated the development of such rapid and agile hopping locomotion. More important is that this manner of feeding would not necessitate the extreme modification of the limbs and girdles to execute the jump into flight so characteristic of this bat. The habit of feeding from backs and necks of the large domestic animals of man is probably an opportunistic utilization of a relatively new and more abundant food source.

During the downstroke of the initial flight following a jump, up to 80 per cent of the area of the wings is configured to provide thrust. The same large muscles of the pectoral girdle that provide adductive power in jumping are able to power at least the first half of a deep downstroke that initially supplies high thrust and subsequently supplies both lift and thrust vital to initiation of forward flight. The upstrokes in initial flight occur ahead of the body and are terminated in a pronounced flick that provides additional thrust and positions the wing for a subsequent downstroke. The first few wingbeats following a jump into flight illustrate that thrust and lift production are the result of the acceleration of air backward and downward by movement of the wings. The amplitude and directionality of the wingbeat, and the velocity and configuration of the wings during the wingbeat cycle, determine the magnitude and direction of the air acceleration. Thus a downstroke could produce almost pure lift or pure thrust depending upon how it was directed and the configuration of the wings. This view contrasts with interpretations of bat flight, which suggest that lift is produced by differential velocity of airflow over opposite sides of the cambered plagiopatagium and that thrust is produced exclusively by the distal chiropatagium. In many of the flights recorded in this study, the distal part of the chiropatagium, the portion often said to be the prime producer of thrust, remained folded as the bat rapidly accelerated. Thrust was obviously being produced by more medial portions of the wing.

Among many evolutionary compromises seen in the vampire bat are the relative shortening of the hand and the retention of a large muscle mass distally in the wing to control the hand movements.

A relatively long hand would be advantageous for lift and thrust production, but would be difficult to quickly fold and unfold in transition to and from terrestrial locomotion, and would be likely to strike the ground on a high amplitude downstroke in the initial flight following a jump. It also would be advantageous to have more muscle mass concentrated near the center of gravity and to have movements in the hand more automatic, as in certain other bats, but the need for independent movement in the hand has necessitated retention of considerable muscle mass distally. The tight folding of the digits during extension of the arm during a jump, and the extended orientation of the digits as the arm is flexed during the first half of the upstroke, are good examples of this independence of movement.

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